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Effects of Air Pollution on Forests: A Critical Review

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16. ABSTRACT

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EFFECTS OF AIR POLLUTION ON FORESTS

A Critical Review

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Atmospheric pollution attributed to increased combustion of fossil fuels has been implicated as a likely contributing factor in observed changes to forests in North America and Europe. Uncertainties surrounding the mechanisms and specific causes for these changes have prompted intensified interest in research on air pollution effects on forests. Major objectives of this review are 1) to provide a conceptual and historical perspective against which today's problems, concerns, and approaches can be evaluated; 2) to evaluate evidence of changes in growth and vitality of some tree species in today's forests; 3) to compare levels of principal atmospheric pollutants in Europe and the U.S.; 4) to describe mechanisms, pathways, and concentration thresholds for effects of principal pollutants on tree growth and physiology; 5) to summarize current evidence for the role of pollution in observed forest declines; and 6) to provide some perspectives on future research in this area. Evidence from laboratory and field research is examined to provide a basis for evaluating the role of atmospheric pollution in present and potential future forest responses.

While the potential influences of atmospheric pollution on forests have been recognized for more than a century,[1] the intensity and scope of concern over pollution-related forest effects has increased most rapidly in just the past three years. Recent reports of loss of vigor and increased mortality of some forest tree species in several European countries, including West and East Germany, Austria, Poland, Czechoslovakia, Switzerland, France, England, and Sweden,[2,3] as well as in the U.S.,[4] have focused intense interest on documenting the geographical extent, causes, and potential ecological and economic consequences of these changes. Atmospheric pollution attributed to increased combustion of fossil fuels in recent decades has been implicated as a potential contributing factor. An apparent consensus among many western European countries and Canada that observed changes are associated directly or indirectly with anthropogenic sources of SO_2 has led to proposed major reductions in SO_2 emissions by these countries by 1993.[5]

The U.S. has deferred a decision on further reducing SO_2 emissions, based in large part on the uncertainties associated with documenting the magnitude and direction of changes to U.S. forests, a lack of clear documentation of the mechanisms and hence specific causes for observed changes, and the enormous costs estimated for reduction of SO_2 emissions.[6] It is precisely those uncertainties that have prompted intensified interest in research on air pollution effects on forests in both Europe and the U.S. and which are the focus of this review.

Major objectives of this review will be 1) to provide a conceptual and historical perspective against which today's problems, concerns, and approaches can be evaluated; 2) to evaluate evidence of changes in growth and vitality of today's forests; 3) to compare levels of principal atmospheric pollutants in Europe (principally West Germany) and the U.S.; 4) to describe mechanisms, pathways, and concentration thresholds for effects of principal pollutants on tree growth and physiology; 5) to summarize current evidence for the role of pollution in observed forest declines; and finally 6) to provide some perspectives on future research needs in this area. These objectives have provided a structural framework dividing the review into principal topic headings.

In addressing these objectives, evidence from laboratory and field research will be examined to provide a basis for evaluating the potential role of atmospheric pollution in the present deterioration being experienced by some forests in Europe and the U.S. and its potential contribution to future changes. Major emphasis will be placed on experiments with forest species, using near-ambient levels of pollutants. Results of experiments with herbaceous plants will be incorporated where they contribute to voids in information on forest species or provide a conceptual basis for understanding pollution effects on soil-plant systems.

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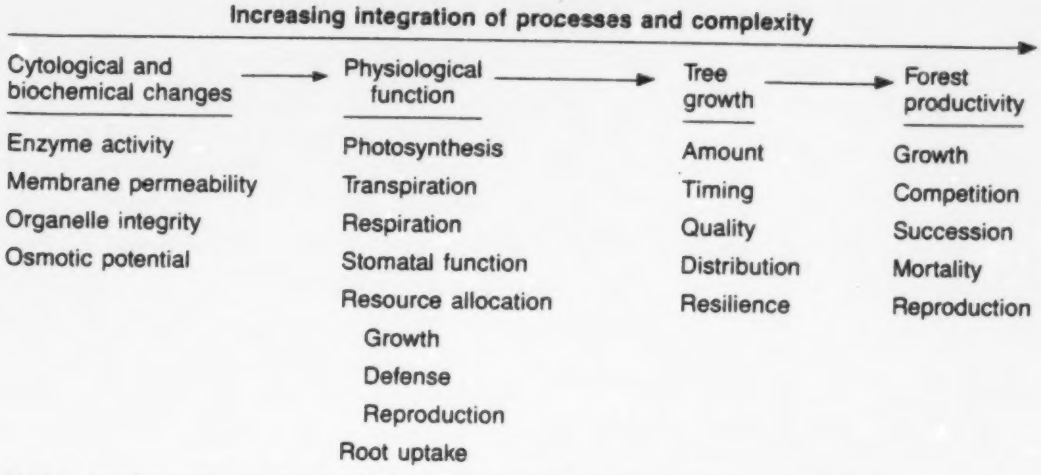

Figure 1. Organizational levels at which air pollutants have been shown to affect growth-related processes of forest trees.

Conceptual and Historical Perspective

Air pollutants can influence forest ecosystems in diverse ways and at many levels of biological organization. Over the past 20 years substantial federal and industrial research effort has been directed toward identifying, quantifying, and predicting these effects on both crops and forests. Until recently, most of this research dealt with gaseous pollutants and trace metals, and much of the focus was on controlled laboratory and greenhouse studies in which the substantial experimental complexities inherent in uncontrolled natural settings are reduced. A conceptual simplification of our present understanding of the principal types of changes induced by air pollutants on forests is presented schematically in Figure 1. The pollutant responses are grouped into four increasingly integrative levels of organization ranging from the initial cytological reactions to changes in growth of forest trees and the productivity of forest communities, a consequence of complex interactions which may involve multiple species of multiple age classes.

Research on pollutant effects on forests represents a paradoxical challenge in the sense that methodologies best suited to understanding the initial reactions on the one hand and the ultimate effects on community productivity and stability on the other are very different. Focusing on either end of the spectrum exclusively ensures that a true understanding of either the causes or the consequences of pollution effects will be ultimately lacking. An appropriate balance between scales of resolution in studies of air pollutant impacts on forests has only rarely been achieved in the past.

Because much of this review will address the nature and potential causes of forest declines, it is appropriate to initially define the term "decline" and examine the principal influencing factors. Declines are complex diseases resulting in a progressive weakening of trees and leading to dieback, the death of portions of the foliated canopy. Gradual loss of vigor involving reduced growth rate and increased susceptibility to secondary biotic and abiotic stresses typically ensues. Declines generally affect mature trees[7] and ultimately, death may occur unless the stress is removed. In recent decades, dieback and decline diseases have killed or damaged millions of trees in the northeastern U.S.[8] Important examples are declines of ash, beech, maple, and oaks.

Manion[7] provided a conceptual framework for considering the role of a variety of stresses contributing to forest declines, as noted in a modified form in Figure 2. In discussing the role of stress in the declines of several tree species in recent decades, he categorized stresses into three classes: predisposing, inciting, and contributing. Predisposing stresses generally have a longer-term role in weakening the tree and making it more susceptible to the shorter-term inciting factors. Examples of inciting factors are the sudden physiological shocks produced by episodic stresses such as insect defoliation or weather damage that may produce abrupt alteration of the

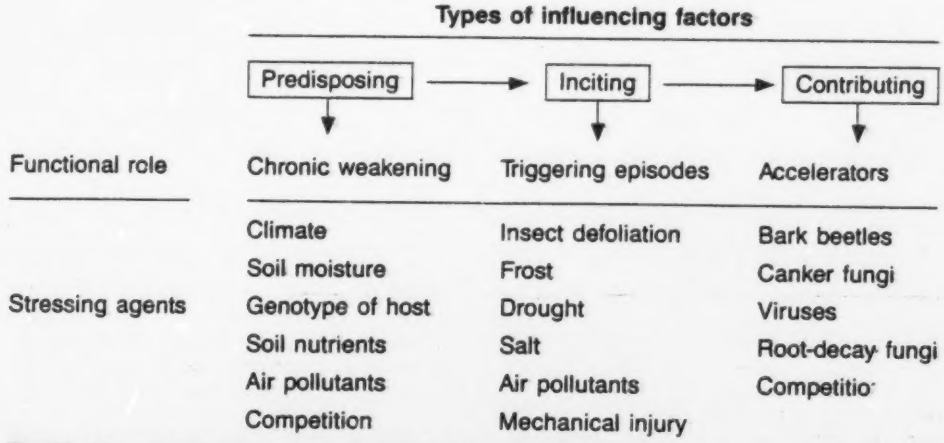

Figure 2. Many categories of factors influencing declines of forest trees (modified after Manion.[7])

tree's physiological condition and make it more susceptible to secondary biotic stresses. Increased susceptibility to biotic stress may take the form of either increased attractiveness as a host or decreased capacity to recover from the stress. Carbohydrate and nutrient supply may play an important role in these changes.[9] Once a tree has begun to decline, contributing factors, which are generally biotic stresses, may ultimately kill or severely weaken the trees by accelerating the decline. These factors are often blamed for the trees' condition when, in fact, they have exerted their role as secondary or tertiary stresses. An additional important factor operating in forest communities is competitive stress, which, in well-stocked forest stands, may have significant influence as either a predisposing or contributing factor in tree responses to anthropogenic stresses.[10]

As noted in Figure 2, air pollutants may act as both predisposing and inciting stresses in influencing declines of forest trees. The potential interactions of pollutant and natural stresses in both of these categories make the development of multiple hypotheses for these declines particularly appropriate. The relative importance of the predisposing and inciting roles of pollutants appears to have changed over recent decades, however, as noted in the following discussion of the types of research historically aimed at understanding pollutant impacts on forests.

The effects of air pollutants on forests have been the subject of several past reviews.[11–14] A major emphasis of many of these reviews and much of our early information on air pollution impacts on forest trees comes from studies near large smelting operations in the first half of this century. Increased mortality, declining vigor, and compositional changes of forests were found over thousands of hectares in the immediate vicinity of these unregulated operations. However, while those studies confirm that pollutants such as SO_2, heavy metals, and hydrogen fluoride can cause severe damage at some dosage level, they provide only limited information of relevance for today's air pollution problems.

The application of abatement technology, increased urbanization and industrialization and the shift to large fossil-fueled electric generating plants with tall stacks have altered both the nature of air quality problems and the type of research needed to address those problems. The major focus has shifted from site-specific studies of the effects of gaseous pollutants occurring along well-defined concentration gradients around individual point sources to evaluation of effects of chronic exposure to multiple pollutants from multiple sources within regional airsheds. More recent reviews[4,15–19] have focused on the effects of longer-term exposure of forests to multiple pollutants at concentrations that may cause subtle alterations of many processes within these ecosystems. Included among these pollutants are wet and dry deposited strong acids. The recognition that strongly acidic rainfall, an apparent product of long distance transport and transformation of sulfur and nitrogen oxides from fossil fuel combustion, is occurring over increasingly large areas of the eastern U.S.[20] has added significant new dimensions to the nature of both potential changes in forest productivity and appropriate methods of their evaluation. Because acid rainfall has the potential to affect forests through both short- and long-term reactions involving soil-mediated processes (nutrient loss or gain[21] and mobilization of trace elements[22]) as well as through direct contact with living tissues,[23] the complexity of the task of assessing effects of regional-scale pollution has increased substantially.

While specific pathways and processes will be discussed in detail later in this review, it should be stated at this point that a clear consensus regarding primary mechanisms responsible for observed forest declines has not yet emerged. This may be attributed to several possible causes, including the lack of long-term monitoring of pollutants in affected areas, the relatively recent focus of research on current problems, the lack of standard methods to address these problems, and the enormous complexity of interactive pathways involving multiple pollutants and genetic and environmental modifiers. Direct extrapolation from traditional laboratory and greenhouse studies to field situations is difficult, and field investigations are hampered by the lack of suitable control sites located outside the influences of regional-scale atmospheric pollution.

Both the above noted complexities and the scale at which forest damage has occurred in recent years have increased the relevance of an additional research tool, the forest survey. As amply demonstrated by three successive surveys in West Germany,[24,25] documentation of the nature and pattern of changes across existing gradients in pollution and other environmental variables can be an important research tool both for evaluating the changes and for drawing inferences about possible causes. The types of changes and the pollution regimes associated with those changes are discussed below.

Regional-Scale Changes in Forest Vigor

Substantial changes in the health of some forest species have been reported in industrialized countries in Europe and the northeastern U.S. and in the relatively pollutant-free environments of the western Pacific. These changes provide a basis for evaluating the possible roles of both anthropogenic and natural environmental stresses in the development of the observed symptoms.

European Forests

Beginning in the early 1970s the occurrence of an unexplained foliar disease on European silver fir was noted in West Germany.[24] The disease appeared initially on older trees and over widespread areas, some of which were remote from centers of industrial activity. While these foliar symptoms, including yellowing and loss of needles, were initially considered to be due to drought, the rapid spread of the disease to other species (e.g., Norway spruce) and to diverse sites across extensive areas of the country, and the lack of recovery of affected individuals, led to the initiation of a country-wide survey of damages in 1982. This initial, preliminary survey led to an estimate that approximately 8% (560,000 ha) of Germany's forest area showed symptoms of damage. Silver fir and Norway spruce were the most severely affected species, with 60% and 10% of the growing stock showing damage symptoms (damaged trees had ≥10% foliage loss), respectively. Subsequent, more systematic surveys showed that areas of damage had increased to 35% in 1983 and 52% in 1984.[25] These increases can be attributed partially to an intensification of the survey techniques with each successive year, but also to a real increase in the extent and severity of effects, based on a subsample of areas surveyed by the same techniques in both 1983 and 1984.[25] With each successive survey, both the diversity of symptoms and the number of affected species increased. Of particular interest and concern in the 1984 survey results was the approximate doubling of areas where hardwood species such as beech and oaks had been affected since the last survey (see Table I). While most of the affected area fell in the slightly damaged category (10–20% foliage loss) during both years, the percentage of area in moderate to severely damaged categories increased by about 80% in 1984.

Some dominant characteristics of the generalized decline phenomenon have been summarized by Cowling.[26]

1. Symptoms of decline occur principally on fir and spruce, beech and pine, but also on the hardwoods including birch, larch, maple, alder, ash, and oaks.
2. Both natural and planted forests are affected.
3. Effects are seen at high and low elevation and on all aspects, but are most pronounced on northwest-facing

Table I. Extent and recent changes in foliar damage to five tree species in West German forests as determined by annual surveys in 1983 and 1984.[25]

	Species distribution area showing damage in 1984[a]				
	Total area affected (10^6 ha)	Damaged/undamaged area (%)		Percent increases 1983–84[c]	
		All damage	≥ Moderate[b] damage	All damage	≥ Moderate damage
Spruce	1.477	51	21	24	86
Pine	0.866	59	21	32	87
Fir	0.152	87	57	16	18
Beech	0.631	50	12	92	168
Oak	0.269	43	9	187	327
Others	0.303	31	8	82	−5
Total	3.698	50	18	47	80

[a] Damage classifications were as follows based on percent loss of foliage: 0–10% healthy, 11–20% light damage, 21–60% sick, 61–99% very sick, 100% dead.
[b] Moderate damage comprises all trees with ≥21% foliage loss.
[c] Change in damage area between the 1983 and 1984 surveys as a percent of area classified as damaged in 1983.

slopes in northwestern Germany and on west-facing slopes above 800 m in the Black Forest of Baden Wurtemburg in the southwest.

4. While effects have generally been most pronounced on older trees, they can be found on all age classes in many areas.
5. Symptoms can be found on stands growing in soils of high or low fertility and on both basic and acid soils (pH range from as low as 3.5 or less to 8.0).

The range of effects noted was quite diverse, including yellowing and premature loss of needles from conifers that resulted in a thinning of the canopy from the inside out, changes in growth patterns of shoots, reduced numbers of fine roots and associated mycorrhizae, a reduced amount and distribution of annual radial growth, and increased mortality.[26] A number of the symptoms are of the type that can be produced by hormonal imbalances, including loss of apical dominance, occasional shedding of green leaves and shoots, and abnormal branching patterns.

The multiple theories of causation for observed forest declines in Germany represent an integration of inferential evidence based on the timing, distribution, and spread of the symptoms determined from the annual damage surveys, disciplinary perspectives of various groups of highly qualified scientists investigating the problems, and a growing body of evidence from field and laboratory experiments engendered by an active and rapidly expanding research program.

The survey results and the various schools of scientific thought share one common thread, that air pollutants (principally sulfur dioxide, heavy metals, nitrogen oxides, and photooxidants) are playing a role in the observed changes.[24–26]

Drought, frost, harmful biotic organisms, and silvicultural treatments are thought to interact in varying degrees as modifying factors with air pollution to produce the observed symptoms. The principal theories advanced to explain forest damage[25] include an interesting mixture of mechanisms and pathways, none of which are mutually exclusive. While these ideas will be discussed in more detail later, they are highlighted at this point as evidence of the conceptual, biological, and chemical complexity of the problem being addressed. Included among the principal hypotheses of causation are: 1) The *aluminum toxicity* theories of Ulrich and coworkers[22,27] consider initial damage to occur as a consequence of increased mobilization of aluminum and heavy metals by combinations of anthropogenic (sulfuric and nitric inputs for the atmosphere) and naturally generated pulses of acidity within the soil profile.[22] Death of fine roots induced by aluminum toxicity is regarded as a primary predisposing condition leading to a variety of secondary symptoms associated with reduced uptake of nutrients and water by functionally impaired roots. 2) *Gaseous pollutants*, principally ozone, are considered by Prinz and coworkers[28] to explain the sudden appearance of foliar chlorosis over much of the region in 1981. They base their evaluation on regional concentrations of ozone and SO_2, the patterns of injury observed, and laboratory exposures with pollutant mixtures in which foliar symptoms were produced similar to those observed in the field. 3) *Foliar nutrient deficiencies* of magnesium observed in the field by Rehfuess[29] led to the concept that low soil availability and/or increased foliar leaching of magnesium induced by acid deposition and perhaps enhanced by ozone are primary factors involved. 4) The *general stress* hypothesis[30] considers the initial stress to be a consequence of impaired photosynthetic capacity induced by air pollutants taken up by foliage. Subsequent symptom development, including production of secondary metabolites and growth hormones, reduced translocation of carbohydrates to roots, and impaired root development and function, are regarded as a consequence of a general disruption of whole-plant carbohydrate economy.

Yet another hypothesis emerged from a scientific exchange of German and American scientists involving reciprocal visits to field sites in areas of forest decline in both countries during the summer of 1984. Based on observations of symptoms of damage across sites with widely different soil nutrient status and widely varying soil and rainfall acidity, this group of soil, plant, and atmospheric scientists discussed the possibility that the high levels of atmospheric deposition of nitrogen occurring across much of Germany may be contributing to the observed symptoms. Mechanisms discussed included direct toxicity from high atmospheric inputs of nitrogen, an imbalance in physiological activity between shoots and roots included by foliar absorption of wet and dry deposited nitrogen, and predisposition to secondary stresses such as low temperatures induced by increasing nitrogen supply to foliage. Such a hypothesis offers some interesting opportunities for experimental testing and, if substantiated, some important implications for emissions control strategies.

Many of the theories and evaluations of forest damage in Germany are based on widespread and synchronous appearance of visible foliar symptoms. Frequently neglected in the assessment and in its scientific explanation is the documentation of growth reductions evidenced in the tree rings. Tree ring records for some areas in Germany indicate that for species such as Norway spruce or silver fir, a slowdown in growth, determined by examination of increment cores, in some cases began 20 or more years ago.[31,32] In this regard, the observed growth patterns bear some similarities to those observed on silver fir in Switzerland,[33] on Norway spruce in southern Norway,[34] and on red spruce in the northeastern U.S.[35,36]

United States Forests

In the U.S., symptoms of forest decline are neither as diverse nor as well developed as those in the forests of West Germany. Research during the past decade has focused more on the chronic effects of gaseous pollutants on species and community-level responses. In one of the earliest regional surveys in a several hundred square kilometer area of the Cumberland Plateau near an industrial corridor in eastern Tennessee, a thorough study of areal extent, symptomology, and pathological basis of decline and mortality of white pine in the 1950s by the U.S. Forest Service,[37] and subsequently by Ellertsen *et al.*[38] of the Tennessee Valley Authority, led to the conclusion that atmospheric conditions in the area were causing the decline. Subsequent studies reviewed by Gerhold[39] revealed that atmospheric pollutants, principally O_3 and SO_2, can be primary causal agents in the development of foliar symptoms of the type observed on pollutant-sensitive white pine trees throughout much of the northeastern U.S.

In one of the few investigations aimed at documenting responses of forest communities to multiple pollutants, McClenahen[40] examined seven deciduous forest stands located along a gradient of chronic air pollution stress on a 50-km portion of the heavily industrialized Ohio River Valley. The diversity of species present was generally reduced for both overstory and understory layers in the forest as proximity to industrial air pollution sources increased. These responses are typical of forest community responses to pollutant stress documented around smelting operations, which eventually lead to a simplification of community composition.[41]

Responses of mature and seedling trees and native herbs have also been documented in the regional atmosphere of the rural northeast. In a series of studies aimed at quantifying the effects of ambient levels of ozone on forest species in the remote Shenandoah National Park in Virginia, Skelly and coworkers[42] documented widespread oxidant effects on sensitive species. Their assessment was based on foliar symptomology (320 trees) and radial growth trends (30 trees) of white pine, measured differences in growth of tree seedlings grown in ambient air and in air purified by charcoal filtration, and measurement of high oxidant concentrations throughout the area (hourly O_3 maximum 250 $\mu g \cdot m^{-3}$, annual average = 100 $\mu g \cdot m^{-3}$). In the latter studies, height growth of tree seedlings and biomass of native herbaceous species were reduced when air was not previously purified by charcoal filtration.

The most comprehensive investigation of the influences of photochemical oxidants on natural forest ecosystems was conducted by Miller and his coworkers in the San Bernardino Mountains of California during the 1970s.[43] Easterly flow of air from Los Angeles has produced very high ozone concentrations in the San Bernardino and San Gabriel mountain ranges, with visible signs of ozone damage being apparent as far as 120 km from the center of the city. Integrated multidisciplinary studies in this pine and mixed conifer forest documented the occurrence of foliar injury, premature leaf fall, decreased photosynthetic capacity, and reduced radial growth. Reduced carbohydrate production and nutrient retention resulted in weakened trees, which became more susceptible to pine bark beetles, increased mortality, and changes in species composition in the more heavily impacted areas.

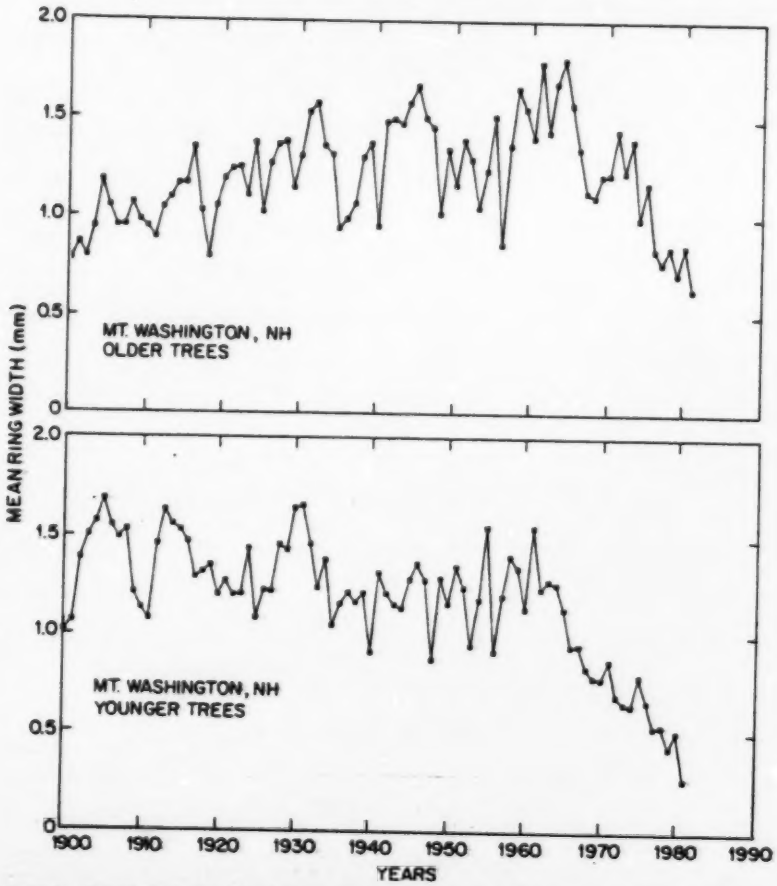

Figure 3. Growth rate comparisons between the 10 youngest and 10 oldest red spruce trees (2 cores per tree with average ages of 84 and 226 years, respectively) at Mount Washington, NH, showing simultaneous radial growth declines. (Compiled from data of T. G. Siccama *et al.*[54,55])

With the recognition that substantial areas of the northeastern U.S. have been exposed to strongly acidic rainfall for at least two to three decades,[20] there has been increased interest in documenting spatial and temporal changes in tree growth within the region. One of the earliest studies of this type by Whittaker *et al.*[44] used total harvest and stem analyses to measure temporal changes in total forest productivity on a series of plots on the Hubbard Brook forest in New Hampshire. Reductions in productivity of approximately 18% between the 1956–1960 and 1961–1965 intervals were found. Both drought and influences of acid deposition were considered possible causes. A second study by Cogbill[45] comparing trends in growth of beech, yellow birch, and red maple collected in New Hampshire with growth patterns of red spruce from the Great Smoky Mountains in Tennessee was also inconclusive. Analyses of tree ring chronologies up to 1973 indicated that no synchronized regional decrease in radial growth had occurred. Slight decreases in basal area increment during the most recent 10 years of these chronologies were observed but the trends were considered inconclusive. Subsequent tree-coring studies revealed an unexplained pattern of growth decline of red spruce in New York[46] and pitch and shortleaf pine in New Jersey[47] during the last two decades.

In the New Jersey study, a strong statistical relationship between annual variation in stream pH and growth rates was evaluated as a basis for considering that acid precipitation may have been a growth-limiting factor for the past two decades.[47] Stream pH in this poorly buffered soil system was closely correlated with precipitation pH during a 36-month period of concurrent records. Of the 345 trees examined, approximately one-third showed normal growth, one-third showed noticeable abnormal compression of annual increments during the past 20–25 years, and the remainder showed dramatic reduction in annual growth over this interval. This effect was evident in trees of different species and at different sites and occurred regardless of age or whether trees were planted or native. Drought has also been considered to play an important role in triggering this growth decline in the late 1950s,[36] but the continued slow growth of many trees since that time appears somewhat unusual.

During the past three years, there has been increased recognition and documentation of decreased growth and vigor of red spruce at numerous locations throughout the Appalachian Mountains. In the initial report by Siccama *et al.*,[35] a 1979 resurvey of 141 red spruce plots in the Green Mountains of Vermont revealed that spruce in these virgin stands at mid to high elevations had decreased in basal area and stem density by about 50% since the initial survey in 1964. Sustained decreases in growth rates were noted in all size classes of this species, which comprised 10–20% of the total basal area of the stand. Symptoms included browning and loss of needles from the top and outside of the canopy downward, a pattern distinctly different from that observed on Norway spruce in Germany where needle loss typically occurs initially from the inner portions of the canopy. Neither the type nor the distribution of effects noted was considered to strongly support climatic changes, root diseases, or stand dynamics as principal causes.[35] Balsam fir, a major component of these forests, appeared vigorous but also showed a decrease in ring width similar to that in spruce.

A subsequent regional survey of spruce decline in 22 stands distributed along the Appalachian Mountains from New Hampshire to North Carolina[36] documented highest mortality (up to approximately 55%) and a higher percentage of spruce with dieback symptoms in northern (boreal and transition) forests than in the southern Appalachians. Mortality, which occurred in all size classes, was highest at higher elevations in northern forests but poorly correlated with elevation of southern sites where generally less than 10% of the stems were dead. Examination of the annual growth rings from increment cores from approximately 700 trees showed that a rapid shift to very narrow rings had occurred in approximately 40% of the trees in the early to mid 1960s with little evidence of recovery; 20% showed suppression in the 1960s followed by normal recovery; and 40% were not obviously affected during this 15 to 20-year period.[36] Subsequent examination of additional southern stands of red spruce and Fraser fir in Virginia,[48] Tennessee,[49] and North Carolina[50] documented similar patterns of reduction in annual growth rings of both high-elevation species beginning around 1960. In the Great Smoky Mountains the patterns of growth reduction of red spruce is less pronounced or absent from lower elevation sites.[51] Similar abrupt changes in ring width of shortleaf pine around 1960 have been observed at lower elevation sites in Tennessee.[49,52]

In Table II, data on the timing and magnitude of radial growth changes from 48 red spruce stands analyzed as part of a multispecies exploratory study of regional growth patterns[53] are summarized. The radial growth curves from which these data were compiled showed a distinctly nonrandom distribution of the timing of initial downward deflection of the ring-width series, with approximately two-thirds of the stands initiating a sustained downard shift in the ring-width series in the interval 1956–1960. Examples of the abrupt shift in radial increment patterns for the 10 youngest and oldest red spruce sampled at Mount Washington, N.H. (Figure 3), demonstrate the synchrony of changes occurring for trees differing in mean age by approximately 140 years. Composite ring-width series for each state sampled in the network (Table II) show the progression of radial growth slowdown during the past two decades. Mean radial growth was approximately 30–50% slower during the past 10 years than in a standard 30-year reference period (1932–1961) and was clearly not consistently influenced by stand age.

Also shown in Table II are comparative data on changes in basal area increment of the subset of stands in each state for which tree diameter data were available. These data, which express changes in cross-sectional area of the tree, show much more emphatically the differences in growth changes between northern and southern spruce (data for Tennessee excepted). Some of these differences are due to age differences between the stands being compared (see table notes for discussion of differences in units of growth description).

These data represent responses of dominant surviving trees which the data of Siccama *et al.*[35] suggest may have been the faster growing, more vigorous trees at the time of his initial survey in the Green Mountains in 1964. They also include the influences of all of the natural stresses which normally influence forest growth, including the effects of canopy disruption in northeastern sites where mortality is high and the micrometereology of the stands has been altered by changing stand structure.[36]

A recent review of the symptomology, ecology, and distribution of red spruce decline in the northeastern U.S.[19] indicated that previous forest declines were reported for some spruce stands in the northeast during the last part of the 19th century. However, the spruce tree ring records examined[55] indicate that the present decline is unprecedented in its synchrony and consistency across the region. Its occurrence on young and old trees on stands with a wide spectrum of ages, basal areas, and prior history of disturbances (including virgin stands and those cut as recently as the early 1900s) argues strongly against natural competitive pressures being a principal initiating stress.[55] The severe drought of the mid-1960s which affected much of the northeastern U.S.[56] has been suggested as a potentially important triggering factor for northeastern spruce decline[37] and cannot be discounted. The initiation of the downward growth trend in many northeastern sites prior to the driest years (1964 and 1965) and its occurrence at southern sites where droughts were not apparent[50] or out of synchrony with the initiation of the downward trend[49] argues against drought as a primary casual agent.

During the past year the U.S. Forest Service has reported an approximate 25% slowdown in radial growth in pines in the

Table II. Historical changes in growth rate for red spruce in the Appalachian Mountains.

State	Number of stands	Age ($\bar{X} \pm 1\ s_d$)	Percent change in mean growth compared to 1932–61		
			Radial increment[a]		Basal area increment[b]
			1962–71	1972–81	1972–81
Maine	4	101 (±10)	−32 (±11)	−35 (±13)	−8 ± 56
New Hampshire	9	123 (±27)	−25 (±15)	−48 (±13)	−19 ± 68
Vermont	6	144 (±24)	−36 (±19)	−53 (±16)	−27 ± 68
New York	8	129 (±15)	−32 (±22)	−51 (±15)	−25 ± 74
West Virginia	3	85 (±3)	−40 (±12)	−57 (±7)	−47 ± 23
Virginia	11	86 (±30)	−36 (±13)	−51 (±20)	1 ± 75
Tennessee	3	172 (±15)	−21 (±1)	−35 (±13)	−10 ± 31
North Carolina	2	57 (±12)	−33 (±3)	−45 (±17)	22 ± 76

[a] Radial increment data were calculated for 1–2 cores per tree for 7–50 trees per stand. Basal area increment data were derived from two cores per tree from approximately 15 trees per stand and four stands per state except TN and NC (two stands each). Sampled stands ranged from near sea level at the Maine coast to 6000 ft (TN and NC). Most were high elevation boreal forests. Data are from trees sampled by Johnson and Siccama,[36] Adams *et al.*,[48] and collaborators with McLaughlin *et al.*[53] Mean ages for the basal area trees were generally ≤5 years different from those for the larger radial increment sample.

[b] In comparing changes in basal area increment (BAI) the age and diameter of the trees during the reference period becomes extremely important. BAI of very young trees will, of course, be extremely low and subsequent basal area growth will increase dramatically even if radial growth declines abruptly, as was the case at Mt. Mitchell, one of the two stands sampled in North Carolina. The within-stand variability is also substantially increased when historical growth changes are expressed in BAI units. Thus, age stratification is clearly important with BAI whereas radial increment is more independent of age (see above and Figure 3) but not linearly proportional to volume growth.

Piedmont regions of South Carolina[57] and Georgia.[58] Changes were substantially less in coastal areas. These reductions, which occurred across all size classes of pines and were accompanied by increased mortality were detected as a part of the periodic National Forest Inventory by which trends in U.S. forest growth and land use are evaluated every 10–12 years.[59] The observed changes have attracted much interest because of the potential implications for valuable commercial forests in these and other southeastern areas. The data are presently being carefully examined to determine the role of silvicultural and climatological influences. The potential influences of air pollutants, particularly photochemical oxidants, on the observed changes eventually must be evaluated even though they must be regarded as speculative at present.

Forests of the Pacific Rim

Canopy dieback and forest decline are also well-recognized and well-developed phenomena across a wide spectrum of indigenous montane forests of the Pacific region[60] The occurrence of these changes in areas remote from significant sources of industrial pollution must be recognized as evidence of the role that natural processes and cycles can play in initiating forest decline and as a basis of comparison with changes occurring in the European and U.S. forests.

Like declines reported in the U.S. and Europe, the Pacific declines occur across a wide variety of soil fertility and moisture conditions. They also occur across a wide range of climatic zones including tropical (Hawaii and Papua, New Guinea), subtropical (New Zeland's North Island), and temperate environments (southern New Zealand, Tasmania, and Australia). They affect principally three tree genera: *Meterosideros*, *Nothofagus*, and *Eucalyptus*. Just as with the European and U.S. declines, there are many theories about primary causative factors. As summarized by Mueller-Dombois[60] from a recent conference devoted specifically to this phenomenon, there are five principal theories of causation based on analyses of field data. These include 1) diseases and animal damage; 2) climate change or perturbation (widely varying annual rainfall levels, cyclonic storms, snow storms, and drought); 3) nutrient limitation (low nitrogen and phosphorus); 4) stand succession (modal populations, cohort senescence); and 5) physiological stress (periodic disruption of the environment of trees growing in areas where they are narrowly adapted physiologically). While there is evidence to support an important role for each of these factors in at least some of the areas where declines have been observed in these forests, the cohort senescence theory of Mueller-Dombois[61] seems to fit many of these situations. Based on the patterns of dieback and their size and continuity, Mueller-Dombois suggests that concomitant senescence of even-aged cohorts of trees occurs in patterns determined by previous catastrophic disturbances such as tropical storms, lava flows, ash blankets, or landslides. These patterns may be repeated but occur with decreasing continuity in successive generations as large numbers of trees reach senescence simultaneously in patches of ever-decreasing spatial integrity.

The diebacks documented in Pacific forests have some significant features that distinguish them from those occurring in U.S. and European forests. First, in almost all cases reported the Pacific declines affect only overstory trees, while European and U.S. forests show effects in all age classes. Second, the effects appear to be confined to a single species at each location, whereas multiple species may be affected in the U.S. and Europe. Finally, the Pacific declines as reported on Hawaii[60] occurred repeatedly in the past and are considered a part of the normal physiognomy of indigenous Hawaiian forests, while those occurring in the U.S. and Europe during the past decade are apparently unique in their range and synchrony across a large region.

At present the Pacific declines are of extreme interest as a documentation of the role of natural stresses on forest successional processes. A role of similar stresses in some of the declining Euorpean and U.S. stands cannot be excluded; however, the above-mentioned differences in etiology suggest that different primary stresses may be initiating the latter declines.

Based on available evidence, air pollutants acting individually or interactively with natural primary or secondary stresses should be considered as potential contributors to the forest declines observed in both Europe and the U.S. The following two sections examine important considerations in-

evaluating the circumstantial and experimental evidence for such a relationship. This evaluation is based both on examining pollution concentrations in ambient air and determining whether chemical and physiological mechanisms of effect have been sufficiently well documented at those levels to explain the observed declines.

over the past 80 years as well as the spatial heterogeneity of those changes in the USA. Total emissions of SO_2 in both the industrialized northeast U.S. and in Europe increased by a factor of about 3 from 1900 levels by 1970. In the eastern U.S. (Table III) and particularly the southeast,[65] the increases have been much larger but have occurred against a background of

Table III. Emission trends for SO_2 and NO_x for the eastern U.S. and Europe.

	SO_2 emissions compared to 1900[a]						Emission density (kg-km^{-2}-year^{-1})[b]			
							SO_2	NO_x		
	1900	1930	1950	1960	1970	1980	1970	1950	1970	1978
Northeast U.S. (PA, OH, NY)	1.0	2.1	2.2	2.3	3.0	2.4	18,254	3,810	8,468	8,650
Mideast U.S. (TN, NC, VA)	1.0	2.7	3.5	5.1	7.3	7.1	5,275	1,410	3,747	4,210
Europe[c]	1.0	1.5	1.4	1.9	2.7		9,800			

[a] Emissions at each interval compared were divided by those for 1900. Data of Gschwandtner *et al.*[62]
[b] Data from EPA.[63]
[c] European emissions after OECD.[64]

Some Concentrations and Patterns of Atmospheric Pollution in Europe and the United States

In the U.S., and to a lesser extent in Europe, long-term monitoring data are not available to determine whether air quality changes have been coincident spatially and temporally with observed forest growth declines. In the absence of these data, both historical trends in emissions and the spatial distribution of atmospheric pollutants have been examined for evidence of the potential role of pollution in recent forest declines. Considerable interest has been focused on comparing pollution levels in the U.S. to those in Europe where damage is more visible, widespread, and generally considered more clearly related to atmospheric pollutants. The data presented in Tables III–VI summarize aspects of air quality for various locations within the two countries, including SO_2 emissions (Table III), acidity of rainfall and cloud moisture (Table IV), concentrations of gaseous pollutants including SO_2, O_3, and NO_x (Table V), and trace metals (Table VI). Because of differences in monitoring protocol from the several studies, both within and between countries, these limited comparisons should be considered as only very general indications of differences in air quality between the study regions.

Emissions and Deposition of Sulfur and Nitrogen

Changes in historical emissions for Europe (SO_2 only) and for selected groups of states in the northeastern and southeastern U.S. (SO_2 and NO_x) are expressed relative to baseline levels of 1960 in Table III. These changes emphasize the rate and magnitude of increases in emissions that have occurred much lower initial levels. An important point of circumstantial comparison is the substantial increase in SO_2 emissions occurring between 1950 and 1970, the period when growth rates of some tree species began to slow markedly in some areas of Europe[31,32] and the U.S.[35,36,49,50] In Europe, SO_2 emissions increased over the 1950–1970 interval by approximately 80% compared to an increase in the U.S. of 110% in the southeast and 40% in the northeast. In the past 10 years, emissions have decreased from a mid-1970s peak to below 1970 levels over much of the northeast. Recent northeastern emissions are at levels only about 5% above those in 1960. In the southeast, SO_2 emissions have continued to increase to present levels which are more than double those in the 1940s and 1950s.[65]

Two important factors not considered by emission trends alone are emission density and changes in the seasonal distribution of emissions. A comparison of trends in emission density in multi-state areas north and south of the Ohio River over the past 100 years[64] indicated a convergence of respective downward and upward emission density trends for these two areas at around 3.5 g S-m^{-2}-y^{-1} in 1980. During the peak emission years around 1970, emission densities for the northeast and southeast were approximately 4.5 and 2.5, respectively, both below the level of 5 g S-m^{-2}-y^{-1} for Europe at that time. Maximum emission densities during the mid 1970s occurred in the Ohio River Valley and exceeded 10 g S-m^{-2}-y^{-1}.[66]

Patterns of sulfur deposition to forests are highly heterogeneous in both the U.S. and Europe. Johnson *et al.*[67] calculated S inputs from wet deposition to range from 4.7 kg ha^{-1}-y^{-1} for Washington in the northwest to 11.7–18.1 kg-ha^{-1}-y^{-1} for three eastern U.S. sites to 24.7 kg ha^{-1}-y^{-1} for a

Table IV. Comparative chemistry of precipitation for selected sites in the eastern U.S. and Europe.

Site	Description	H^+	SO_4^{2-}	NO_3	NH_4	Cl^-	Na^+	Ca	Mg	Reference
		Rainfall chemistry (μeq-L^{-1})								
USA	Avg 17 stations 1978/79 MAP3S/EPRI NE-U.S.	97.7	58.6	25.5	17.2	11.2	15.9			76
USA	New York NADP sites	60.4	64.8	30.2	16.5	5.8	6.2	8.4		77
USA	Walker Branch 1981–83 Watershed, TN	55	54	16	10	7.5	5.2	10	1.6	78
Sweden	Southern, mid-1970s	52	70	31	31	18	15	14	8	79
Germany	Black Forest, SW	51.0	56.9	23.6	16.4	12.1	8.6	10.0	5.7	19
Germany	Landenbrugge, NE	128.1	154.6	66.2	69.1	35.7	24.2	25.6	11.7	19
		Fog and cloud chemistry								
Germany	Black Forest, fog	126	399	390	377	147	270	219		72
USA	Whiteface, NY	280	140	110	89	3.1	11	17		80
USA	Mt. Moosilauke, NH	288	342	195	108		30			71

Table V. Comparative air quality for sites in the U.S. and West Germany.

			($\mu g \cdot m^{-3}$)		Reference
SO_2	Annual average	USA	23–51	Eastern U.S. urban	81
			7–15	Northeast U.S. rural	82
		FRG	10–36	Clean areas	72
			70	Rhine-Ruhr	72
	Shorter term	USA	8–40	Monthly OH, KY, IN	81
			165	Maximum hourly rural East TN, 1981–83	78
			>1000	Maximum hourly urban industrial areas	81
			277	Maximum daily, Hof	82
		FRG	13–20	Monthly Bavarian Forest	72
			300–1900	½-h max NE Bavaria	83
			500	Several hours average	83
O_3	Annual average	USA	57–96	Remote sites	84
		FRG	60–90	Clean areas	72
	Maximum hourly	USA	255–911	Ohio	85
			313–802	Pennsylvania	85
			196–334	New York	85
			666–784	California	85
			98–245	Remote sites	84
		FRG	208	Black Forest	72
			358	Bavarian Forest	72
			410	Rhine Ruhr	72
NO_2	Annual average	USA	4–19	Northeast	81
			50–150	Urban areas	81
		FRG	2–3	Clean areas	72
			30–60	Industrial areas	72
	Shorter term	USA	28–73	Maximum hourly rural east	81
		FRG	33	Maximum daily Schauinsland	82

central European forest. Total deposition of sulfur for central Europe is in the range of 30–60 kg S $ha^{-1} \cdot y^{-1}$.[68]

Nitrogen oxides have been estimated to contribute approximately 25% of the strong acidity to rainfall in the northeastern U.S.[69] and 19% of the acidity in West German rainfall.[70] Emissions of nitrogen oxides have increased substantially in the eastern U.S. during the past 30 years (Table III). During the interval 1950–1978 NO_x emissions more than doubled in the northeast while those in the southeast tripled. Emission densities in Europe in 1970 were substantially higher than those in the southeastern U.S. but only about one-half those in the northeastern states.

Present levels of deposition of nitrogen in precipitation range from 4 to 10 $kg \cdot ha^{-1}$ for the northeastern states,[4] but may be substantially higher at high-elevation sites such as Mt. Moosilauke,[71] where cloud and bulk precipitation inputs of nitrogen combined were 35.6 $kg \cdot ha^{-1} \cdot y^{-1}$. In West Germany, annual deposition values for nitrogen range from 17 $kg \cdot ha^{-1}$ in the north-central Solling Forest to values as high as 73 $kg \cdot ha^{-1}$ in the northeast.[72]

In addition to trends in overall emissions and deposition, a consideration of the seasonality of those trends is of particular interest where biological effects are concerned. It has been suggested that both annual emissions and annual precipitation acidity may mask important seasonal variations in these variables, particularly summertime values.[73] This observation is of particular relevance to evaluating the potential for emissions to influence the growing cycle of deciduous forest trees. Analyses of the seasonality of emissions of SO_2 indicate that while annual SO_2 emissions decreased in recent years, the summertime emissions of SO_2 have continued to rise markedly. Consequently, emissions decreases have not been accompanied by decreases in the acidity of summer rainfall in the northeastern U.S.[73]

Precipitation Chemistry

Precipitation chemistry data summarized in Table IV from several sites in the U.S. and Europe indicate that concentrations for most ionic species in the precipitation of northeastern U.S. sites are generally comparable to those recorded in the German Black Forest, an area where substantial damage has been documented. By contrast, considerably higher concentrations of most constituents, particularly NO_3 and NH_4, were

Table VI. Comparative total deposition of four heavy metals from diverse sites (after Lindberg *et al.*[86]).

Location[a]	Airshed type	Total atmospheric deposition ($mg \cdot m^{-2} \cdot year^{-1}$) Cd	Mn	Pb	Zn
Greenland	Remote	0.006	0.022	0.06	0.17
Georgia, USA	Rural	0.72		8.8	
Tennessee, USA	Rural	0.5	22	15	8.9
Vermont, USA	Rural			52	18
Maine, USA	Rural			20	15
Solling, Germany					
Beech forest	Rural	1.6		44	163
Spruce forest	Rural	2.0		73	173

[a] Sources cited by Lindberg *et al.*[86]

measured in precipitation from Landenbrugge in northeastern West Germany. Average annual volume-weighted pH of rainfall in most of the northeastern U.S. is 4.1–4.3,[74] while West German precipitation has monthly values which range from 4.0 to 5.6 (mean 4.5) in clean areas to 3.9–5.1 (mean 4.3) in areas of higher industrial activity.[72] It should be noted that, in examining these mean values, substantial variations can occur from these values both on temporal and spatial scales.

Forest vegetation may also intercept substantial amounts of moisture from exposure to clouds and fog. In Germany, it is estimated that fog is present up to 150–200 days per year in Bavarian and Black Forests.[72] In the Green Mountains of the northeastern U.S., Siccama[75] observed that the boreal spruce forest is at or above cloud level for 900 to approximately 2300 hours per year. Chemical analysis of fog collected in the Black Forest and cloud moisture from two northeastern U.S. mountains indicates much higher concentrations of most ionic species in the German fog; however, the pH of cloud moisture is noticeably lower in the U.S. in this limited comparison.

Gaseous Pollutants and Heavy Metals

The comparison of atmospheric concentrations of SO_2, O_3, and NO_2 in Table V focuses on rural and urban sites and on both annual and shorter-term averaging intervals. Gaseous exposure regimes in West Germany and the U.S. appear to be in the same general concentration ranges, with SO_2 somewhat higher in Germany and O_3 higher in the U.S. By contrast, a comparison of total wet and dry deposition of four heavy metals at four rural eastern U.S. locations, a remote site in Greenland, and the Solling Forest in West Germany (Table VI) indicates that total deposition of all four metals is substantially higher at the European site.[86] Deposition of cadmium, manganese, and zinc was an order of magnitude higher at the German site, and lead deposition at that site was 40–73% higher than at any of the four U.S. sites. Atmospheric inputs of all four of these heavy metals are two to four orders of magnitude higher than those at the remote sites in Greenland.

Trends in emissions and atmospheric concentrations of pollutants are of little interest from a biological perspective unless pathways and mechanisms by which forest systems interact with the pollutants are established and reaction thresholds are shown to be in the range of concentrations and exposure durations typical of ambient environments. The next section examines the principal pathways and concentration thresholds for pollution impacts on forest systems.

Principal Pathways and Mechanisms of Pollutant Impacts on Forests

Pollutants may influence forest growth and development through multiple pathways and mechanisms and over widely varying time scales. Effects may be direct due to contact with plant surfaces, resulting in impaired physiological capacity

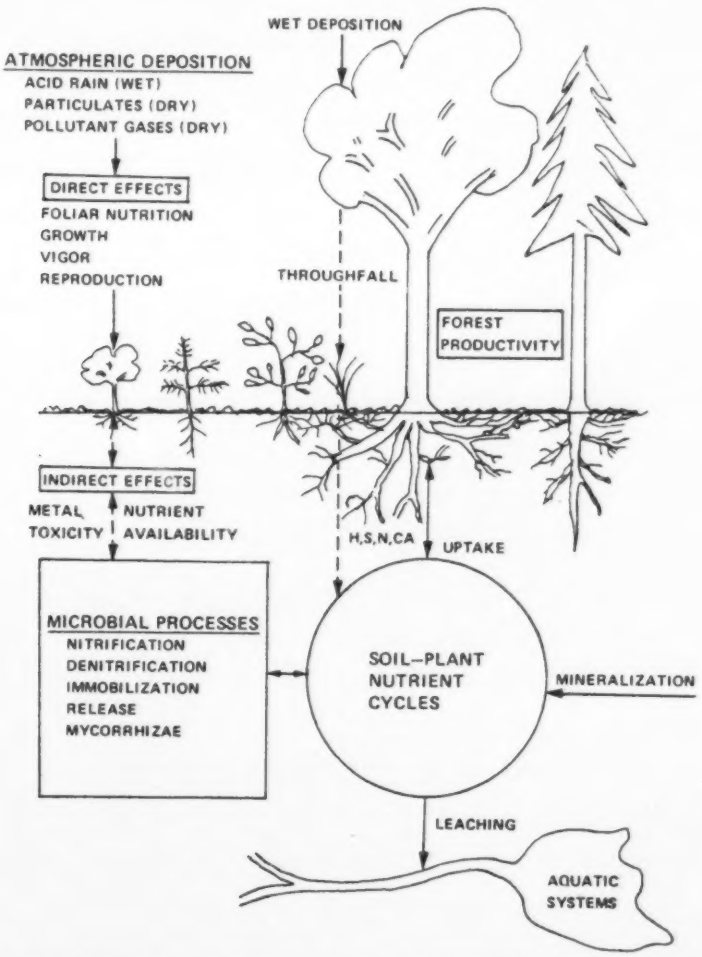

Figure 4. Conceptual diagram of sites of reaction of wet- and dry-deposited atmospheric pollutants on forested ecosystems.

of shoots, or indirect as a consequence of altered availability of nutrients or toxic metals. Altered susceptibility to a variety of secondary biotic and abiotic stresses may also be induced by pollution stress. Pollutants may interact additively, antagonistically or synergistically, depending on the specific pollutants involved, their concentrations and the exposure conditions. Effects may be induced by short exposures to high concentrations (acute effects), or chronic exposures to lower pollutant levels resulting in cumulative and likely interactive stresses. Environmental variables including temperature, humidity and radiation levels, as well as plant variables such as species, growth stage and nutritional status have been shown to strongly influence plant response to a given pollutant dose (concentration × time). While short exposures to high pollutant concentrations may cause more damage than the same dose delivered at lower concentration over a longer time period,[87] lower level chronic exposures are generally more representative of today's regional-scale conditions.

A conceptual diagram of the principal pathways by which pollutants interact with forest systems (Figure 4) emphasizes the interactions between the soil/plant processes that control the rate and direction of forest growth and succession. It is important to recognize that forest water, nutrient and carbon cycles are closely coupled in forest ecosystems and that the interrelationships among the pathways by which these resources are acquired and utilized make determination of initial sites of reactivity, and hence principal causative factors in forest responses, difficult to ascertain.

Direct Effects of Gaseous Pollutants

Effects of gaseous pollutants are primarily a consequence of their diffusion through the stomatal pores of foliage, dissolution in water in the mesophyll cells of the walls of the substomatal cavity and subsequent alteration of a wide variety of biochemical and cytological processes that ultimtely affect plant growth and development.[88,89] Interpretation of relevant processes and pathways and evaluation of the significance of results of much of the past controlled fumigation work with both gaseous pollutants and acid rain are complicated by the use of unrealistic combinations of high pollutant concentrations and exposure times. Roberts[90] reviewed data from field and controlled experiments with trees and suggests an approximate long-term concentration threshold of 100–150 $\mu g \cdot m^{-3}$ for growth effects of SO_2 on forest trees, although he cites several studies where annual average concentrations in the range of 40–60 $\mu g \cdot m^{-3}$ have adversely affected conifers. Damage at SO_2 concentrations below those associated with visible injury to the foliage is well documented for forest trees, particularly conifers.[91] Foliage on the most sensitive genetic clones of white pine have been visibly injured by a few hours exposure to 65 $\mu g \cdot m^{-3}$ SO_2 when combined with 98 $\mu g \cdot m^{-3}$ O_3.[92]

Ozone is one of the most significant gaseous pollutants because it occurs at phytotoxic concentrations over broad areas of Europe[93] and the U.S.[94] While long-term monitoring data for ozone are not generally available in the U.S., there are longer-term records for Europe which indicate ozone concentrations presently being measured represent an approximate doubling of values recorded in 1956.[95] Of particular importance in ozone reactions with plant systems is its capacity to attack cellular membranes, thereby altering their permeability and the integrity of cellular organization.[88] Chronic damage may occur with sensitive species at mean levels as low as 120 $\mu g \cdot m^{-3}$ while exposures of a few hours at 100–160 $\mu g \cdot m^{-3}$ can produce visible injury.[93]

Results of controlled exposures of tree seedlings to low-concentration mixtures of gaseous pollutants indicate that synergistic reactions may play an important role in the reactivity of the pollutant mix. Seedling shoot growth of yellow-poplar, for example, was unaffected by 35-day exposures to SO_2 (160 $\mu g \cdot m^{-3}$) or O_3 (140 $\mu g \cdot m^{-3}$), but combinations of SO_2 + O_3, SO_2 + NO_2 (190 $\mu g \cdot m^{-3}$), or SO_2 + O_3 + NO_2 reduced shoot growth 51, 64, and 51%, respectively.[95] High phytotoxicity and synergistic activity of the combination of SO_2 and NO_2 was also noted in exposures of broad-leaved tree seedlings.[97] In the latter experiment both the cumulative effects of exposures over more than one growing season and the significance of dormant season exposure to SO_2 and NO_2 on subsequent leaf growth were demonstrated.

The preceding discussion of concentration thresholds combined with data on ambient pollutant concentrations (Table V) can provide a basis for evaluating the likelihood that current ambient levels are in a range which might adversely affect forest trees. On this basis, direct effects of SO_2 would be expected in industrial but not rural areas of Germany. In the U.S. effects would be anticipated only in the vicinity of large urban complexes or near point sources but not in remote areas. Ozone effects by contrast appear highly likely across large areas of both the U.S. and West Germany because of the regional distribution of this ubiquitous pollutant. Maximum hourly concentrations exceed short-term (hours to weeks) damage thresholds by factors of 2–9 at the various locations compared. Nitrogen dioxide does not appear to exceed a general damage threshold for individual or combined effects in either country. It should be noted that these comparisons are for regional data and that local hotspots for all of these pollutants may occur around industrial or urban areas. On a regional scale, however, only SO_2 in Europe and O_3 in both countries appear to be in the concentration range of likely effects.

Exposure of forests to gaseous pollutants occurs most commonly in areas receiving precipitation which, on an episodic basis, may be 10 to 100 times more acidic than the theoretical "background" pH of 5.6.[69] Interative effects of gaseous pollutants and acid rain on forest trees are generally not well understood and may occur through virtually any of the pathways conceptualized in Figure 4. A wide array of effects of acid rain *per se* have been suggested as possible;[98] however, there is at present only limited documentation of direct effects of rainfall acidity on plant growth at ambient pH levels.[23] The evidence from the field of alteration of normal growth processes in declining forest trees suggests several principal physiological mechanisms of action[99] as discussed below.

Some Likely Physiological Mechanisms of Effect for Observed Forest Responses

Altered Plant-Water Relations

Several recent studies suggested that tree growth-climate relationships in the northeastern U.S. and Europe may have been altered during recent decades.[47,100–102] Such relationships can be induced by a variety of stresses including both climate itself and physiological disruptions of plant-water relations by air pollutants.

Altered plant-water relations can result from either diminished capacity of the plant to take up water from the soil or a loss in capacity to control water loss to the atmosphere from foliage. A likely mechanism for decreased water uptake potential is a reduction in biomass of fine roots. Reduced root function can be caused by either 1) direct toxicity induced by soil chemical changes associated with increased inputs of acidity, or 2) reduced translocation of carbohydrates from pollution-damaged shoots. Evidence of direct toxicity to fine roots in European forests resulting from soil acidification was presented by Ulrich *et al.*[22] They hypothesized that a 90% reduction in the fine root biomass of a 120-year-old beech forest during a dry summer in Germany was due to a buildup of aluminum and iron to toxic levels in the soil as a result of increased anthropogenic and natural acid production.

Although rapid turnover of the fine root biomass is part of natural cycles for some forests,[29] there is ample evidence of high sensitivity of plant-root systems to a variety of trace metals,[103] many of which increase in availability as soil acidity

increases.[22,104] In addition to direct effects on root biomass, soil acidification may result in changes in availability of cations, particularly calcium, necessary for proper root growth and normal physiological function. Physiological and histological studies support the importance of adequate calcium levels for growth of meristematic tissues and proper membrane development and stability.[105,106] In general, stresses that reduce the capacity of aboveground plant systems to produce photosynthate at a rate required for growth and development of these tissues will result in reduced allocation to root systems and a consequent decline in root vigor.[9] Gaseous air pollutants, particularly ozone, can alter partitioning of biomass between plant parts[107] and interfere with translocation of photosynthate to root systems.

In addition to effects on water supply to shoots, changes in cuticular integrity and changes in stomatal function by pollutants may alter plant capacity to regulate transpirational water loss. Acid rain and associated pollutants can alter leaf surface characteristics, principally through weathering or chemical alteration of cuticular waxes.[108] At present, neither the mechanisms (whether reduced wax production or increased weathering) nor the physiological significance of cuticular alteration by acid rain have been adequately characterized. Field studies with Scots pine in Finland[109] indicate that erosion of cuticular waxes was 2–5 times more rapid in areas of higher atmospheric pollution. Wax layers around the stomates were particularly susceptible. Fowler *et al.*[110] compared rates of alteration of cuticular waxes of Scots pine needles in polluted (wet plus dry deposition) and relatively less polluted sites in the field and found that mainly qualitative (structural) rather than quantitative changes had occurred. It was estimated that the observed changes would affect plant-water status and subsequently plant productivity (≤5%) only during dry periods. Horntvedt *et al.*[111] found no effect of irrigation with pH 2.5 H_2SO_4 on cuticular wax of Scots pine, Norway spruce, or lodgepole pine, however. These results suggest that cuticular changes observed in the field may occur only as a result of a longer term of exposure of foliage to pollutant combinations rather than single pollutants such as acid precipitation.

The effects of gaseous pollutants on stomatal function are well documented from laboratory studies under controlled environmental conditions.[89] In general, high levels of either SO_2 or O_3 cause stomatal closure, which may protect plants from further pollutant entry and from water vapor loss. However, under low levels of SO_2 (26 $\mu g \cdot m^{-3}$) and low relative humidities (≤40%), stomatal opening was enhanced in bean (*Vicia faba*), particularly when plants were previously drought stressed, a factor that could intensify plant-water stress under these conditions.[112]

Increased uptake of potentially toxic trace elements such as aluminum and iron[22,113] is an additional apparent result of increased exposure of soil and foliage to acid deposition. Because movement of the more mobile trace metals such as aluminum occurs in the transpiration stream, these elements can be expected to be concentrated near sites of evaporative loss of water and, hence, buildup in and around the guard and subsidiary cells of the stomates may occur. Accumulation of trace metals in these tissues may lead to altered physiological control of stomatal action and potential changes in leaf-water balance. Increased stomatal resistance has been reported for peach seedlings, which also showed decreased root volume when grown in nutrient solution with aluminum concentrations of 46 $mg \cdot L^{-1}$.[114] Vogelman[115] reported that transpiration in spruce seedlings can be reduced markedly even by low levels of aluminum in nutrient solution.

Changes in Forest Nutrition

There are two principal mechanisms by which acid deposition may alter nutrient status of forest trees: 1) altered availability of nutrients from the soil, and 2) atmospheric addition or depletion of nutrients in foliage.

Several recent reviews examined the evidence for acid rain effects on forest productivity via alteration of availability of soil nutrients.[21,112,116,118,119] In general, the negative effects of acid rain on forest soils are considered to be related to displacement of calcium and magnesium from upper soil horizon or from reduced microbial decomposition and release of nutrients from soil organic matter.[22] On the other hand, positive effects may occur where nitrogen inputs in acid rain represent a significant addition to available nitrogen in soils.[116] The potential losses of nutrients from soils due to leaching by acid rain must be considered in relation to 1) the available pools of nutrients in the soil and vegetation, 2) natural leaching losses from internal acid production by trees and microorganisms, 3) rates of resupply of nutrients from mineralization of soil organic matter and weathering of minerals, and 4) nutrient uptake and incorporation into woody biomass.[67] Information on weathering rate and plant uptake is deficient in many of the attempts to budget net nutrient losses from soil systems.

Soil acidification and cation leaching are not necessarily synonymous.[117] Leaching without acidification may occur where weathering of primary minerals is rapid enough to resupply the system with cations. On the other hand, acidification without leaching may occur if both H^+ and its associated anions (SO_4 or NO_4) are immobilized in soil.[120] For these reasons, soils vary widely in their potential sennsitivity to acid rain.[119] From a nutritional standpoint, soils of intermediate pH and fertility may be most sensitive to significant acid rain induced changes.[15] Soils which are already acidic and poorly buffered may be more resistant to further losses of nutrients but more susceptible to mobilization and increased availability of aluminum and other trace elements for both uptake by vegetation and leaching to aquatic systems.[121] Ulrich *et al.*[22] hypothesized that anthropogenic sources of acidity combined with natural soil generated pulses of acidity during warm, dry years represent critical stress periods for forests. The significance of acid pulses and associated increases in trace elements for forest trees was questioned by Rehfuess,[29] who pointed out that some tree species have adapted to survive on acid soils in the presence of high levels of Ai, Mn, and other heavy metals.

Forest growth *per se* has an acidifying influence on the forest environment because of uptake of base cations and the release of hydrogen ions by root systems.[122] Johnson *et al.*[123] have estimated that anthropogenic inputs of acidity have approximately doubled internal acid production in the soil by trees in deciduous forests in eastern Tennessee. Available soil reserves were estimated to be adequate for 50–70 years of removal at these rates even in the absence of inputs from weathering. A potentially important difference between natural and anthropogenic inputs of acidity, however, is that anthropogenic additions occur in episodes, whereas natural production is a more gradual process.[122]

The significance of nutrient losses from soils to growth and associated physiological processes of forest trees has not been well quantified. It is known that there are large differences in nutrient requirements between tree species.[116] Nitrogen, magnesium, and calcium deficiency may occur in tissues at concentrations that are generally 1.5 (N) to 6 (Ca) times higher in birch than in Norway spruce, for example.[116] Because growth-limiting nutrient levels are not adequately documented, the development of a dose-response curve for expected forest growth losses versus nutrient loss from the soil would be extremely difficult for most nutrients, with the possible exception of nitrogen and phosphorus. This is partly a function of inadequate experimentation and partly attributable to the fact that growth will be most limited by the nutrient in lowest supply relative to growth demands at that time; and thus nutrient response surfaces can be very complex.

With acid deposition the complexities of potential effects on forest nutrition are increased by nutrient exchange within

the canopy itself.[67,124] A comparison of chemical inputs in bulk precipitation to throughfall contents of pine and hardwood canopies (Table VII) indicates that either canopy enrichment or canopy depletion of nutrients can occur as a result of atmospheric inputs and that these effects vary both among chemical elements and between species types.[124] Of particular interest in Table VII is the nitrogen enrichment (approximately 0.6 $kg \cdot ha^{-1} \cdot y^{-1}$) of hardwood canopies, while conifer canopies experienced small net nitrogen losses (approximately 0.8 $kg \cdot ha^{-1} \cdot y^{-1}$). Leaching losses of SO_4, Ca, and Mg occurred to varying degrees with both forest canopy types. The significance of these losses to the physiological function of foliage will, of course, depend on rates of replenishment from the soil, as well as on the overall nutritional adequacy of initial plant tissue levels. Miller[125] considers that replacement mechanisms are sufficiently rapid to resupply nutrients leached from plant leaves unless tissues are changed by additional stresses such as ozone. An analysis of the comparative data on deposition, canopy exchange rates, and annual growth requirements for major nutrients for forest stands in Europe and the U.S.[126] indicates that potassium is also highly leached. Annual leaching losses from the canopy for this element were equal to 71% of the annual nutrient requirements of Norway spruce in the Solling Forest of West Germany. Calcium losses were 38% of annual requirements. The combination of cation losses (particularly K, Ca, and Mg) from foliage and reduced cation availability and/or uptake from soil suggests that leaching induced by acid precipitation might ultimately impose a stress to some forest systems.[116]

Table VII. A comparison of canopy exchange of selected constituents with incident bulk deposition in two forest types in New York (after Mollitor and Raynal).[124]

Constituent	Bulk input ($kg \cdot ha^{-1}$)[b]	Canopy exchange ($kg \cdot ha^{-1}$)[a]	
		Hardwood	Conifer
NO_3–N[c]	3.45	+0.58	−0.78
SO_4–S[c]	8.69	−1.37	−7.76
H	0.70	+0.31	+0.09
Ca	1.65	−12.07	−14.91
Mg	0.40	−1.24	−1.72
Na	0.68	−0.03	−0.09

[a] Exchange calculated as either a net loss (−) or a net gain (+).
[b] Amount in 100 cm of bulk precipitation from May 2, 1979, to May 7, 1980.
[c] In the case of NO_3 and SO_4, low estimates of dry deposition in bulk input and high estimtes of throughfall contents would result in overestimating losses and underestimating gains by the canopy, particularly for NO_3–N. Lindberg *et al.*[86] estimate that uptake of nitric acid vapor may account for ≥50% of dry-deposited nitrogen for forest canopies.

Liming of forests with calcium and magnesium has been considered as a possible remedial treatment to alleviate soil acidification. Widespread liming of German forests began in the 1950s to promote litter decomposition and remineralization. A review of the process and its efficiency for alleviating forest damage indicates that only a small part of forest damage in Germany has been stopped by liming.[127] While acidification of soils may be reduced for a while, aboveground damage continued and the potential damage of the ecosystem from heavy doses of lime is great.[127]

The importance of calcium and magnesium was emphasized recently by observations of severe deficiencies of these elements in foliage[29,128] and roots[32] of Norway spruce in Germany. Both impaired uptake and acceleration of leaching losses have been implicated as causal factors. Laboratory studies in West Germany designed to examine interactive effects of O_3 and acid mist show that increased foliar leaching of magnesium can be induced by exposure to ambient levels of these atmospheric constituents.[28] Nutrient losses from trees generally increase with the acidity of rainfall. Among the nutrients lost from foliage are the carbohydrates, which are the major constituents leached from foliage. Generally, the leaching rates are higher for deciduous trees than for conifers and higher in mature leaves than in younger tissue.[129]

Leaching losses of nitrogen from foliage may be inconsequential relative to increased nitrogen inputs. Johnson *et al.*[67] compared atmospheric inputs of nitrogen to nitrogen requirements for a variety of forest types and found that in or downwind of areas of relatively high emissions from fossil fuel combustion such as Tennessee, New Hampshire, and West Germany, atmospheric inputs of nitrogen comprised a minimum of 31% of annual nitrogen requirements for northern hardwood forest in New Hampshire to a maximum of 269% of Norway spruce requirements in Germany. Such estimates are based on bulk deposition measurements that may underestimate actual deposition (dry and wet processes) by a factor of 2 or more.[86] Thus estimates of canopy retention based on differences between bulk inputs and throughfall may be low.

Excessive levels of nitrogen input in German forests and at high elevation sites in the eastern U.S.[71] constitute a potential stress to normal growth because balances in growth between roots and shoots may be disrupted by direct fertilization of the canopy. In addition, excess nitrogen inputs may ultimtely result in increased soil nitrification and consequently in soil acidification as a consequence of internal NO_3 production by microorganisms in the soil.[130] At present, adverse near-term nutritional effects of acid rain on forest growth are considered unlikely under most conditions because of the size and turnover rates of soil nutrient pools. From a physiological standpoint, better characterization of the sites, mechanisms, and metabolic effects of nutrient exchange in the canopy would greatly aid in the process of evaluating the significance of altered nutrient exchange to the whole soil-plant system.

Effects on Growth and Reproduction

Results of experiments with simulated acid rain. A wide variety of acid irrigation experiments were carried out to evaluate the effects of acidification on Scandinavian forests. Abrahamson[116] reviewed many of the Scandinavian and U.S. studies on the effects of acid rain on seedling growth and found no studies in which simulated rainfall of near ambient acidity levels caused negative effects. In many cases, effects on growth were stimulatory. In most of these studies positive growth responses were attributed to the fertilizing effects of added sulfur and nitrogen.

Seedling establishment is generally more sensitive to soil acidity than seedling growth and generally decreases rapidly below a soil pH of 4.4.[116] A wide range in sensitivities of seeds of northeastern U.S. forest species to substrate acidity was demonstrated by Raynal *et al.*[131] Maximum germination for white pine, for instance, occurred in the 3.0–2.4 pH range. Germination of red maple and yellow birch was inhibited, while hemlock was unaffected by pH levels in the 3.0–4.0 pH range, which is not uncommon for pH of throughfall below the canopy.[125] Mechanisms discussed by Raynal *et al.*[131] as potentially responsible for the observed response were associated with osmotic effects of the subtrate solution as well as its ionic characteristics. Both of these solution properties can lead to leaching of metabolically active substances from seeds, with possible adverse physiological effects.

Direct effects of rainfall acidity on the flowering physiology of forest trees have received relatively little attention to date. *In vitro* assays to determine the sensitivity of pollen of 13 Canadian forest species to moisture droplets acidified with dilute H_2SO_4 indicated that the LD50 for pollen germination of broad-leaved canopy species during 3-h exposures was in the pH range 3.95 to 3.6,[132] well within the range of episodic ambient rainfall events. Pollen tube elongation for an herbaceous forest species, *Oenothera parviflora* L., was found

to be more sensitive than germination in inhibition by simulated rainfall, with significant reduction in elongation being produced by pH levels as high as 4.6.[133] It should be noted that inhibition of conifer pollen germination has also been reported in controlled studies following fumigations for 16 h with concentrations of SO_2 as low as 195 $\mu g \cdot m^{-3}$, a level exceeded in industrial areas of Europe.[134] Reductions in seed production, seed weight, and pollen germination have also been reported for white and red pine growing in areas of high ambient air pollution.[134]

Many acid irrigation experiments in the field involving larger saplings and trees were also conducted in Sweden and Norway.[136] In Swedish experiments,[137] young (18-year old) Scots pines were irrigated below the canopy with dilute sulfuric acid (50–150 $kg \cdot ha^{-1}$ H_2SO_4 in one application per year), both with and without prior addition of fertilizer. After six years of annual application, a negative correlation between treatment acidity and basal area growth was found on the fertilized plots (10% decrease at highest acidity), whereas growth response was positive (approximately 30% increase at the highest acidity level) on the unfertilized plots. Increased nitrogen uptake was considered a probable cause of positive responses. Results of these studies were complicated by changes in nutrient availability in the soil associated with the direct effects of high acidity on soil fungi, bacteria, and competing understory vegetation,[137] as well as by the absence of contact with the canopy by the simulated rainfall.

In Norwegian experiments,[138,139] a variety of combinations of acidified groundwater treatments (pH values between 6.0 and 3.0 by H_2SO_4 addition), treatment volumes (25–50 $mm \cdot month^{-1}$) application techniques (below or above canopy), lime applications (500–4500 kg $CaO \cdot ha^{-1}$), and tree species (lodgepole pine, Norway spruce, silver birch, and Scots pine) were used. The overall effects of these experiments after four to seven years of treatment applications were small where found.[140] In studies with Scots pine, positive growth effects were found at pH levels of 3.0, 2.5, and 2.0 after four years of treatment, followed by a significant growth reduction by pH 2.0 in the fifth year. Norway spruce showed reduced diameter growth of all acid treatment levels in the year following the cessation of six years of prior treatment. Height growth of silver birch was stimulated by rainfall acidity. Lime application had little or no effect on observed responses. Effects of acid irrigation on foliar nutrient levels were also generally small.[140]

In evaluating the results of the Scandinavian irrigation experiments, Abrahamson[116] concluded that the data give "no substantial evidence of effects on tree growth at acidity levels presently found in precipitation." However, he cautions that the acid effects produced, particularly at the highest acidity levels, may be partly attributable to soil effects that were artifacts of the highly acid treatment levels and hence not representative of longer-term responses to be expected under actual field conditions.

Numerous studies have also been conducted to determine dose-response relationships and varietal sensitivity of crop plants to simulated acid rain.[141,142] In general, growth reductions of field-grown agricultural crops have not occurred at pH levels above 3.0. Increased growth of crop species has been found at pH levels as low as 3.0 and 2.8 in greenhouse and field experiments, respectively.[141] An interesting bimodal response to rainfall acidity has been noted in some greenhouse experiments with crops with negative growth effects at around pH 4.0 being supplanted by positive effects at higher acidities.[143] Differential sensitivities and influences on whole-plant responses by roots and shoots has been suggested as one possible explanation.[99] Thus while shoot-mediated responses may be a dominant influence at intermediate pH treatments, nutritional inputs and soil changes may play a dominant role as treatment acidity is increased further. Additional experiments to examine root and shoot-mediated responses at ambient rainfall acidity levels are needed.

In reviewing possible mechanisms for direct effects of acidity on foliage, Jacobson[141] discussed direct effects of hydrogen ion on biochemical reactions, including enzyme activity and cell wall elongation. Such effects are plausible physiologically because the acidity of cell sap is normally maintained within a relatively narrow pH range necessary for maintenance of enzyme configuration and reactivity.[144] While plant cells have buffering mechanisms to deal with excess acidity, the limits to which those systems may be stressed by ionic changes imposed by losses of Ca^{2+} and Mg^{2+} and gains of H^+ during canopy reactions with acid rain are not known. Strong acids may also substantially change the properties of cell walls, including accelerating the loss of calcium and loosening the cell wall fibers, with a resultant loss of cell osmotic potential.[88] The importance of atmopsheric deposition of pollutants on this process at ambient levels has not been determined. In spite of the existence of such mechanisms, experiments conducted to date with most forest species give little cause for concern about direct adverse effects of present rainfall acidity *per se* on tree growth.

Heavy metal toxicity. Heavy metals, which may be deposited and/or increased in availability by dry and wet deposition, have the potential to significantly affect forest ecosystems through multiple pathways. Their potential significance is based on regional increases in availability in rainfall,[104] recent accumulations in litter and soil,[145,146] long residence times in soil systems,[146] and inherent toxicity to plant growth processes.[103,148,149] The mobilization of aluminum in forest soils by soil acidification processes[22] has focused considerable attention on possible effects of acid rain on availability of a variety of trace metals to forest trees. Several mechanisms for increased availability exist. These include increased wet and dry deposition to vegetative surfaces and soil; increased availability of foliar-deposited materials through either altered cuticular surface characteristics or increased (acid-induced) chemical availability on the leaf surface; and increased chemical mobilization in soils as a function of soil acidifying reactions. In reviewing the potential phytotoxicity of trace elements released by coal combustion, Vaughn *et al.*[150] list the following principal considerations: 1) emission rate, 2) dilution level in endogenous soil pools, 3) bioaccumulation rate, and 4) toxicity. The interplay of factors controlling chemical and biological availability and ultimately biological affects is still poorly understood, however. Studies of distribution patterns of trace elements in spruce in the German Black Forest indicate that lead, cadmium, and copper accumulate mainly from atmospheric inputs, manganese from the soil, and zinc from both sources.[151] The relative contributions of wet:dry deposition of trace inputs to a deciduous forest may vary widely for different elements, ranging from a minimum of 0.1 for manganese and 0.8 for lead to 3–4 for cadmium and zinc.[152] Trace metal mass balance measurements in several deciduous forest watersheds indicate a significant net retention of many toxic metals with estimates of retention ranging from 20–70% for manganese to 88–99% for cadmium, lead, and zinc.[153]

The potential for trace elements to accumulate in forest systems is high due to both long residence time and multiple paths of entry into forest trees. Hutchinson[147] lists residence times in soils ranging from 280 years for cadmium to 2100 years for zinc and 6300 years for chromium in the Upper Thames Basin in England. Friedland *et al.*[146] recently reported a 148% increase in lead in the organic horizons of forest soils in the Green Mountains of Vermont during the past 14 years. Copper and zinc had also increased in approximate proportion to deposition rates during that time span.

A budget of the distribution of lead and zinc in a forested watershed in eastern Tennessee[154] indicated that the distribution of these elements may vary widely among tissue types (15–45×) as well as among tissues of the same type for different species (3–6×). In general, elemental contents de-

creased in the following order: O_2 litter > O_1 litter > fine roots > large roots > leaves > branches > bole. The between-species range in lead and zinc concentrations ($\mu g \cdot g^{-1}$) for foliage [2.7–7.8 (Pb) and 10–36 (Zn)] and bole wood [0.4–2.8 (Pb) and 3.5–14 (Zn)] was generally in the same range as intersite concentration ranges reported for Norway spruce in the Solling and Bärholde Black forest in Germany (0.6–5.4 for lead and 27–34 for zinc in foliage; 1.0–7 for lead and 20–21 for zinc in wood, respectively).

Increased deposition and availability of trace elements in forest soils has raised questions about changing availability of these elements to trees and whether the trees themselves might provide a historical record of anthropogenic inputs. Radial patterns of trace element accumulation in shortleaf pine tree rings in eastern Tennessee[155] for example, show increasing tissue levels of several elements including Zn, Al, Cu, Fe, Cr, and Ti during the past two to three decades which may reflect increased recent deposition and/or availability of these elements. Substantial differences in accumulation occurred between species and concentrations of these elements were generally 10 times higher in the cambial zone than in most recently formed xylem. A comparison of concentrations in wood formed before 1955, and the produced from 1977 to 1983, and concentrations in the cambium/phloem area is shown for selected elements in shortleaf pine in Table VIII. In examining these changes, it should be pointed out that some elements such as zinc and aluminum may be relatively mobile and be translocated to more active tissues.[157] Thus, higher levels in recent tissue may reflect longer-term accumulation patterns for these elements. Other elements such as iron and chromium are considered to be relatively immobile in plants and may be good indicators of both historical changes in deposition levels and present day availability. The data of Baes and McLaughlin,[52] for example, indicate that levels of Fe in tissue increased sharply in Cades Cove in the Great Smoky Mountains of Tennessee during the operation of the smelters (1855–1910) at Copper Hill 88 km (55 miles) upwind. Tissue levels dropped sharply after 1910 when litigation terminated open-pit roasting and when sulfur recovery units were installed. Recent patterns of increase in trace elements in shortleaf pine at several locations in Tennessee[52,155] show 1) levels of iron in xylem comparable to or above levels found in Cades Cove during the late 1800s, and 2) levels of decrease in radial growth during the past 25 years comparable to those observed during the period of maximum smelting activity (1800–1900).

There is still much to be learned about the relationship between growth rate and the levels of trace elements ultimately incorporated into wood; however, the relatively high levels of several elements in the cambium/phloem area of particular interest from the standpoint of potential direct effects of these elements on growth and physiological processes in these metabolically active tissues.

The most critical problems in determining trace element toxicity to forest trees is quantifying individual and combined trace element concentration thresholds for toxicity. Determining a toxic threshold for tissue levels of trace elements is complicated by the fact that some metals may act either directly or indirectly through their influence on other nutrients. Aluminum, for example, may reduce phosphorus or calcium availability.[149] Aluminum may also replace calcium and magnesium in cell walls because of its much greater affinity for pectins.[27]

A comparison of concentrations of elements in nutrient solutions that induce deficient, normal, and toxic reactions in seed plants[148] (Table IX) indicates that several of these elements including Cd, Cu, Cr, Fe, and Pb, have solution toxicity ranges that overlap that of Al. Of more interest from a field assessment standpoint are the tissue contents at which toxic reactions occur. Unfortunately, there are very limited data on the soil and tissue concentrations at which metals become toxic to trees in forest soils. It is known that there are substantial differences between species and soil types with respect to the toxicity of available aluminum. Experiments in the U.S. with tree seedlings cultured in nutrient solution indicated that toxic thresholds may be rather high (10–160 $mg \cdot L^{-1}$) for aluminum.[158,159] For Norway spruce, by contrast, the damage threshold was 1.0–2.0 $mg \cdot L^{-1}$ [160] and the maintenance of a Ca:Al ratio ≥ 1 was considered essential to minimize root damage. Considerable lower threshold concentrations have been noted for agriculture crops where the aluminum toxicity of acid soils is a well-recognized problem. A comparison of aluminum toxicity to cotton in soil solutions from various southeastern U.S. soil horizons[161] indicated that toxicity was highest for some B horizons, with soil solution concentrations thresholds as low as 0.01 $mg \cdot L^{-1}$. Aluminum in upper soil horizons was 20–330 times less toxic, presumably because of the formation of organic complexes.

Because of the uncertainties of influences of elemental ratios and rhizosphere reactions in nutrient solutions, the levels of trace elements in tissues may be a more realistic indicator of toxic thresholds for comparisons of laboratory and field experiments. Aluminum concentrations in peach seedlings growing in a 3 $mg \cdot L^{-1}$ aluminum solution, for example, were 700, 48, and 113 $\mu g \cdot g^{-1}$ in roots, stems, and leaves, respectively, and were associated with reduced growth of both shoots and

Table VIII. Dry weight concentrations ($\mu g \cdot g^{-1}$) of potentially toxic metals in shortleaf pine collected in eastern Tennessee.

Site/tissue	Al	Cd	Cu	Fe	Mn	Zn
Phloem & cambium						
Oak Ridge area	200–690	0.47–7.5	1.9–3.0	5.2–180	180–450	30–83
GSMNP[a]	220–610	0.54–0.96	2.2–4.1	17–21	150–240	27–130
1978–1983 Xylem						
Near KSP[b]	8.1–36	0.21–0.33	1.5–2.4	47–77	53–100	77–260
Oak Ridge area	5.4–27	0.059–1.1	0.55–1.1	1.3–9.8	24–81	3.3–7.6
GSMNP	21–36	0.11–0.22	0.74–2.5	1.1–9.4	27–43	3.7–31
1943–1952 Xylem						
Near KSP	11–14	0.20–0.37	0.61–0.72	11–26	62–100	19–42
Oak Ridge area	3.4–14	0.085–0.49	0.27–0.73	0.50–3.9	7.4–83	3.9–16
GSMNP	4.6–10	0.19–0.58	0.41–0.56	0.43–1.8	16–100	8.3–22
Toxic effects[c]	65–325	2–80	>22	>100 ppm	>400–550	>150

[a] Great Smoky Mountains National Park.
[b] 1.4 km downwind of Kingston steam plant which burns 4×10^6 Mg coal per year.
[c] Toxic effects thresholds for several different species from references in Baes *et al.*[155] except lower value for Al from Pavan *et al.*[156]

roots.[162] Calcium and magnesium uptake was inhibited by approximately 20% at 10-mg·L^{-1} solution concentrations. Threshold leaf aluminum concentrations of coffee seedlings grown in acid soils were 62 and 100 μg·g^{-1} for inhibition of root and shoot growth, respectively.[156]

Soil solution aluminum levels are generally below those used in nutrient culture studies. Aluminum concentrations in soil leachates in northwestern soils were found to be 0.32 and 0.69 mg·L^{-1} for B horizons from hardwood and conifer forests, respectively, in the Adirondack Mountains of New York[163] and 0.38 mg·L^{-1} for an A_2-horizon percolate from a fir zone forest in New Hampshire.[164] The levels for these northeastern U.S. sites are somewhat lower than the 1–2 mg·Al·L^{-1} reported by Ulrich *et al.*[22] as occurring on a continuous basis in soil solutions in the Solling Forest in Germany. Aluminum concentrations from these forest soil solutions are thus much lower than threshold values for toxicity reported from nutrient culture experiments with tree seedlings, but much higher than thresholds for injury determined by testing agricultural species in soils. The importance of differences in species tolerances and differences in the validity of testing protocols in these comparisons is unknown.

Elemental concentrations in the cambium of various tissues of shortleaf pine (Table VIII) indicate that aluminum, iron, manganese, and possibly zinc are present at levels at or, in the case of aluminum, substantially above foliar levels associated with aluminum toxicity in peach and coffee tree seedlings. Obviously, the gaps in our understanding of the complex interactions between soil type, metal concentration and form, and species differences in tolerance to heavy metals are still very large.

Altered Resistance to Secondary Stresses

Forests are influenced by a wide array of natural biotic and abiotic stresses that alter the allocation of resources to various plant organs and among various biochemical compartments. These influences may exert significant control over a tree's ability to resist disease[7–9] There are several reports of forest trees becoming increasingly susceptible to secondary stresses as a consequence of exposure to air pollutants. A classical example is the San Bernardino Forest in southern California where high photochemical oxidant levels have severely altered forest growth, mortality, and structure.[43] Here, a high degree of association between attack by bark beetles and prior oxidant pollution damage of ponderosa pine was noted.[165] Based on further study of the physiological mechanisms of this response, a variety of physiological changes induced by air pollution stress were hypothesized to have enhanced the susceptibility of ponderosa pine to attack by western pine beetle and mountain pine beetle.[166,167] These included reduction in oleoresin exudation pressure, quality of flow, an increase in the propensity of oleoresin to crystallize, and a reduction in phloem and sapwood moisture content.

In the east, studies in the southern Applachian Mountains[168] demonstrated declining growth of mature white pine trees in three ozone sensitivity classes (tolerant, intermediate, and sensitive) showing variable foliar sensitivity to ambient ozone levels. Excavation of a subsample of the trees that died after repeated development of clinical symptoms of ozone injury revealed infection by root disease fungi. In a comparison of growth and carbohydrate allocation of tolerant and sensitive white pine trees in East Tennessee,[169] sensitive trees were found to have reduced availability of carbohydrates for translocation from foliage, reduced radial growth (70%), and a loss in physiological resilience of the growth process. The latter condition was evidenced by a loss in responsiveness to climatic variations and an inability of the sensitive trees to respond to the "good" years.

Changes in foliar nutrient status may also enhance foliar susceptibility to low temperatures. Rehfuess[170] suggested increased sensitivity of magnesium-deficient Norway spruce foliage to frost damage. Friedland *et al.*[171] noted repeated winter damage to recent needles of red spruce in the Green Mountains of Vermont and suggested that the top to bottom defoliation pattern and declining vigor of these trees may be a consequence of repeated winter damage. Predisposition of these trees to winter injury by atmospheric nitrogen deposition and associated delayed cold hardening was considered one plausible hypothesis for observed symptoms, based on high atmospheric deposition of nitrogen at high-elevation sites in this region and a similarity of cytological symptoms to those associated with heavy nitrogen fertilization of coniferous forests of Europe.

Increased input of atmospherically derived foliar nitrogen may be of benefit to the growth and vigor of trees growing in nitrogen-deficient soils; however, the benefits may be offset if the balance between root and shoot growth is altered. Nitrogen fertilization by soil application can increase the shoot:root ratio of trees,[172] and atmospheric inputs to the canopy may be even more effective in this regard. Rapid absorption of nitrogen applied as foliar fertilizer can occur even when existing levels of foliar nitrogen have been increased by soil-applied nitrogen.[173] Increasing shoot:root ratios, whether induced nutritionally from atmospheric inputs or from reduced translocation of photosynthate from pollutant-stressed shoots,[168] would be anticipated to enhance susceptibility of trees to moisture stress.

There has been little work on the direct effects of acid rain on diseases of forest trees under field conditions. In general, trees weakened by any primary stresses that reduce belowground vigor are likely to experience increased susceptibility to root pathogens.[7–9] In declining red spruce stands in New England, an increasing incidence of the root decay fungus *Armillarea Mellea* was found in all locations examined but root decay was considered a contributing secondary agent on the basis of its being least developed on the most heavily damaged stands at high elevation.[174]

At present, the most direct evidence for acid rain effects on plant diseases comes from studies where simulated rain was applied to both greenhouse and field grown seedlings.[175,176] Simulated rain of pH 3.2 inhibited the rust fungus *Cronartium fusiforme* on willow oak and the root-knot nematode on kidney bean and, depending on the developmental stage of the host and pathogen, caused stimulation or suppression of halo blight of kidney bean.[175] Reduced incidence of both foliar and soil-borne pathogens on field-grown loblolly pine treated with simulated acid rain at approximately ambient pH values has also been reported.[176] Preliminary results indicated that acid rain might occasionally induce infection of the facultatively parasitic pitch canker fungus *Cronartium fusiforme* by causing physical damage that facilitated pathogen invasion. Based on these studies, it was suggested that acidity levels occurring in ambient rain are high enough to alter host-pathogen relationships following a few, or even single, exposures.[176]

Treatment with simulated rainfall at a near ambient pH (4.0) has also been found to reduce the vigor of mycorrhizae[177]

Table IX. Concentrations (mg·L^{-1}) of elements in nutrient solutions affecting growth of seed plants.[a]

Element	Deficient	Normal	Toxic
Aluminum		<0.1	0.1–32
Calcium	0.015–14	0.12–200	>500
Cadium		<0.05	0.2–9
Copper	<0.01	0.01–0.1	0.5–8
Chromium (−4)		<0.5	0.5–10
Iron	<0.5	0.5–5	10–200
Lead		<3	3–20
Sulfur	<0.7	3–270	>8000
Zinc	<0.0006	0.002–0.2	60–400

[a] Source: H. J. M. Bowen.[148]

of loblolly pine seedlings. Changes in uptake of nutrients and water and reduced capacity for growth would be anticipated under these conditions.

Forest Community Responses—An Integration of Processes

Forest productivity and the rate and direction of forest successional processes are controlled by biological, chemical, and physical factors that are integrated at many levels of organization. A major component of these integrated systems is the competitive pressure exerted by both intra- and interspecific competition for carbon (light), water, and nutrient resources. Forest systems, while resilient in many ways, may be strongly controlled by a balance in competitive potential of a few key species. If those species are disturbed by either natural or anthropogenic stresses, competitive shifts may ensue leading to substantial changes in growth of those species and ultimately the composition of the forest.[178] Thus, the difficult task of understanding how individual tree and species-level effects are integrated into forest stand-level responses is pivotal to assessing present changes in forest productivity and predicting the consequences of those changes on the composition of future forests.

Unfortunately there is relatively little information on which to evaluate the consequences of regional air pollution on forest community dynamics.[179] Smith[180] categorized possible effects of pollutants on forest systems as: Class I (low dose), innocuous or slightly stimulatory; Class II (intermediate), longer-term changes produced by subtle stress, which cause structural or functional alteration of the ecosystem; and Class III (high), rapid deterioration of the system leading to major changes in system function and death of individuals.

While the Class I and II reactions are of greatest interest in this country because of the large and valuable forest resource that is potentially within these categories, most of our information on community responses comes from studies in Class III conditions. In general, forests exposed to stress respond by changing in composition to less diverse communities where the later successional, more specialized species are replaced by the earlier successional generalists that can tolerate a broader range of stresses.[181] This process may lead to a reversal of normal successional development, a simplification of the community associated with a reduction in diversity of species present, and a loss of the taller vegetation.

Characterization of forest community responses to chronic pollution stress in both the industrial corridor studies in Ohio[40] and in the oxidant-impacted San Bernardino National Forest,[43] has established reductions in diversity of forest composition as a typical response to pollution stress. The character of the red spruce stands at high elevations in the northeast and Norway spruce and silver fir stands in Germany also has been altered in a manner which is more characteristic of Smith's Class III category. The extent to which these alterations are reversible in some species or able to be offset by species replacement is currently unknown.

The question of whether subtle pollution-induced changes in competition are occurring over larger areas of generally unmanaged forests of the eastern U.S. is still unanswered. Some qualitative aspects of the role of pollution stress on forest competition have been examined using a forest growth and succession model.[10] Forest simulations aimed at exploring the roles of competition, stress level, and time in determining whole-forest responses to low levels of stress imposed at the species level suggest that competition may play a very important role in either compensating for or amplifying the effects of applied external stresses.[10] Responses of individual species in these simulations depended on the growth characteristics of the species and the developmental stage of the forest at the time stress was initiated.

Based on field studies of a mixed oak forest at varying distances from a coal-burning power plant, Rosenberg *et al.*[182] suggested that species richness and diversity may be more sensitive indicators of pollution damage than growth of individual overstory species. However, changes in relative growth rate between species may be useful as indications of subtle changes in competitive potential. A recent field study in eastern Tennessee[183] detected shifts in the relative interspecific competitive potential of yellow poplar and white oak in mixed deciduous stands. These shifts occurred around 1960. Other continuous inventory plots in this area[184] show a sharp reduction in biomass of shortleaf pine and hickory during the past 11 years. Both species show sharp growth reductions in annual ring width in the past 20–30 years and mortality from bark beetle attacks is high. Replacement of pine by yellow poplar occurred in some stands, resulting in no change in total biomass; however, the biomass loss from hickory mortality still has not been compensated for internally. Whether the preceding changes were precipitated by a stress similar to that operating at about the same time in red spruce stands or were merely a consequence of normal successional changes cannot be ascertained at this time.

Conclusions from Past Research

The preceding sections have sequentially examined the nature and progression of forest declines observed in Europe and the U.S.; trends, differences, and similarities in air quality in those regions in which declines are occurring; and finally, principal mechanisms and pathways by which plant processes and plant communities have been hypothesized and/or demonstrated to be affected at pollutant levels in the range of those that occur in the ambient atmosphere or in the soil. The following summary of these areas of discussion is offered:

1. The observed forest declines in West Germany and the U.S. are widespread, sometimes simultaneously affecting more than one species at a site and have intensified over a relatively short time span and across a wide array of stand and tree ages, soil types, elevations, and stand histories.
2. In many instances, trees showing evidence of crown dieback and growth decline experienced a shift to a much slower growth rate 20 to 30 years ago as evidenced by the tree-ring records.
3. The diversity of sites, species, and stand conditions and the consistency of the pattern of observed decline symptoms argue strongly against silvicultural factors, disease, and regional drought as primary stresses in the observed declines.
4. The timing of a shift to slower growth rates in red spruce and Fraser fir in the U.S. and limited similar studies in Norway spruce and silver fir in Europe is generally coincidental with a period of rapidly increasing emissions of SO_2. Circumstantial comparisons of this type should also recognize the possible role of other large-scale changes, particularly climatic changes over this same interval.
5. Based on the limited comparisons from this review, air quality in areas of forest decline in West Germany and the U.S. is generally comparable. Levels of sulfur and nitrogen deposition are generally higher in Germany, while ozone and wet-deposited acidity are somewhat higher in the northeastern U.S.
6. A wide variety of physiological disorders of forest trees have been observed in the field and in laboratory experiments at ambient regional levels of SO_2 (Germany) and O_3 (in Germany and the U.S.). Ambient rainfall acidity *per se* has not been consistently related to the observed symptoms of decline in laboratory or field experiments, but in combination with ozone or in interaction with some soils may be responsible for foliar leaching of Mg and Ca or release of toxic heavy metals to levels that inhibit growth of roots and shoots. The direct effects of very acid

fogs occurring at high elevations have not been adequately evaluated.

7. Based on field irrigation experiments and studies of forest nutrient cycles, short-term negative effects of acid deposition on forest soils appear unlikely. Longer-term potential for negative effects based on influences on balances of weathering, leaching, and microbial mineralization has not yet been adequately evaluated. Positive nutritional effects of nitrogen additions may occur; however, the influence of direct nitrogen fertilization to the canopy may also represent a physiological stress under some conditions, especially at loading levels experienced at high elevations.
8. Heavy metals deposited from the atmosphere or mobilized from soils are of particular concern to forest ecosystems because they may be accumulated in soils or plant tissues, have long residence times, and are toxic to some plant species at soil and plant tissue levels that in some instances may occur in the regional environment.

The preceding observations provide circumstantial evidence of the possible role of atmospheric pollution in initiating or contributing to observed changes in forest vigor. Such evidence is much stronger in Europe where the number of species affected, the diversity of symptoms produced, and the spatial gradients of those symptoms near areas of present and past industrial activity strongly implicate atmospheric pollution in at least some areas. In the U.S., fewer species are obviously affected, symptoms are somewhat different and less diverse, and the most severely declining trees have been observed principally at higher-elevation sites and in the northeast. The pattern of growth decreases observed in red spruce at a variety of sites throughout the Appalachian Mountains supports the concept of a regional-scale environmental stress as a contributing factor. Both atmospheric pollution and regional climate fall in that category, and their influences could be interactive in both atmospheric and biological dimensions.

There are still many postulated pathways and mechanisms for the observed responses, including both direct and indirect influences of O_3, wet and dry deposited strong acids, and heavy metals, as well as climatic change. Many of the mechanisms, particularly foliar leaching of nutrients, reduced carbohydrate production and decreased vigor of roots occur at ambient pollutant levels typical of at least some of the regions where damage has been detected. However, there is still no clear evidence of a single causal agent and, hence, no indication that control of a specific pollutant will be a near-term solution to observed problems. Additional research involving field, laboratory, and modeling approaches is clearly warranted to more clearly define the role of anthropogenic and natural stresses in the observed patterns.

Perspectives on Future Research Needs

As noted in the preceding section, there are still many questions about the nature, causes, and consequences of recent forest declines which have not been adequately answered to date. These uncertainties continue to confront forest ecologists, physiologists, pathologists, and nutritionists with many new and challenging tasks. Several of these tasks offer significant opportunities for better understanding of forest growth processes under natural as well as pollutant-stressed environments. Some major areas of information needed are 1) measuring and evaluating subtle changes in growth processes; 2) defining rates of alteration of soil-plant nutrient cycles; 3) characterizing critical characteristics of gaseous pollution exposure dosages; 4) developing a better understanding of the role of pollutant-pollutant and pollutant-environment interactions in plant response; and 5) integrating process-level changes into projected system-level response. These areas are discussed briefly below.

One of the most important challenges is quantifying the timing and distributions of recent changes in forest growth. Possibly subtle changes in growth characteristics may provide useful early warning signals of more extensive alterations of species and community-level responses to pollution stress. Dendroecology, the study of environmental influences on annual radial growth determined from measured width of tree rings,[185] has been used in a variety of studies to examine long-term changes in growth of trees in polluted environments.[34,56,186–188] It offers a useful technique for rapidly determining the important regional base-line growth rates of trees for time periods preceding the most recent decades of increased atmospheric pollution.

In addition to examining the influence of principal controlling variables on changes in the form of growth curves, there are a number of other statistical properties of the time series of annual ring widths which should be useful in documenting the point of initiation of changes in those curves. Such changes may be important early warning signals because they will likely occur well before the system is visibly and significantly impacted. These include changes in the magnitude of variations in annual growth rate of individual trees over time, differences between individual tree responses within a population of the same species, and variations in responses of different species at the same site over time.[34]

Densitometry, the study of temporal changes in density of wood, can also provide important documentation of the timing of quantitative and qualitative changes in annual growth characteristics. Measurements of changes in wood density may be even more sensitive than ring width measurements in determining stress. Schweingrubber *et al.*[188] have reported reduced maximum latewood density in tree rings from a network of European sites which occurred during the interval 1950–1975, the only such synchronous occurrence in the past 200 years. Conkey[189] has reported similar changes in red spruce density from three sites in Maine with reduced density values being much more evident than reduced ring widths in some cases. While dendroecological and densitometric methods can provide rapid characterization of the timing and scale of growth changes, ultimately, for quantification of changes in total forest productivity, it will be important to quantify changes in all size classes within the forest. For this purpose, some combination of permanent forest inventory plots and coring technology may be most appropriate for documenting both the timing and distribution of changes.

The use of stem analysis procedures to document changes in the distribution of growth along the bole also is being investigated as a technique for obtaining much additional data on tree growth that are not collected in routine dendroecological analysis.[191] Such procedures may be particularly relevant for examining the potential effects of atmospheric nitrogen on growth form of forest trees.

The influence of atmospheric pollution on forest nutrient cycles remains a topic of intense interest for evaluating both short-term (canopy interactions) and long-term (biogeochemical cycles) influences on forest ecosystems. While there is a growing body of evidence to support a role for nutrient leaching from foliage in some nutrient deficiencies observed in declining forests, the mechanisms and speed with which trees compensate for canopy-level nutrient exchange are still not well quantified. Ulrich[192] discusses the role of roots in responding to and regulating calcium levels in foliage. Since foliage and roots are connected along an electrolytic continuum, the "neutralization" of rainfall in the canopy may be accompanied by acidification in the rhizosphere as roots take up base cations and release hydrogen to the soil solution. The rhizosphere itself offers intriguing possibilities for research relative to acid deposition effects. The chemistry in this thin biologically and chemically active zone[192,193] around the active roots may play the dominant role in nutrient and trace element exchange by forest trees, and the presence, absence, or modification of a normal rhizosphere may explain some discrepancies between results obtained in laboratory and field

experiments. Characterization of the chemistry and physiology of root:rhizosphere interactions under the influences of anthropogenic deposition to both plant canopies and soils should be a productive area of future research.

Other relevant research areas include 1) evaluating the role of atmospheric inputs of nitrogen on the allocation of nutrient and carbohydrate resources of associated changes in resistance of trees to secondary stresses; 2) characterizing effects of pollutants on reproductive physiology; and 3) defining the tolerance limits of trees for individual and combined trace metals in tissues. For any experiments considering direct or indirect effects of acid deposition on forests, interactive exposures to ambient levels of ozone will be particularly relevant. Collectively these experiments should embody whole-plant physiological concepts and focus on stress-induced alterations in the distributions of resources between roots and shoots.

Gaseous pollutants, principally ozone in the U.S., have to date been the most demonstrably toxic constituents of regional atmospheric pollution. With respect to effects of gaseous pollutants on forest growth, our understanding of the role of dosage kinetics during diurnal daily and seasonal fluctuations is still inadequate. The importance of the frequency and duration of intervening periods of recovery during low levels of ozone, for instance, is not sufficiently well understood to permit growth changes to be predicted from long-term exposure dosages.[196] Future controlled studies should be directed toward more accurately reflecting these substantial fluctuations. Field chambers which permit side by side comparisons of tree seedling growth in ambient air and air purified by charcoal filtration should be used increasingly to evaluate current impacts of ambient pollutant levels. Such chambers have already been used in a national crop-loss assessment program,[196] which has led to estimates of annual benefits to major U.S. crop species of a 25% reduction in ambient ozone levels of $1.7–1.9 billion per year. While quantifying chamber responses of tree seedlings is very important, it should be noted that physiological balances and sensitivity of tree seedlings in chambers may be very different from those of mature forest trees. Annual growth of commercial forests in the eastern U.S. is approximately 370×10^6 m^3 and economic losses to these forests due to air pollution cannot be accurately assessed with data presently available.[197]

The influences of changes in chemical constituents in the atmosphere, other than those traditionally associated with industrial pollution, may achieve increasing significance in future studies. The stimulatory effects on growth of an approximate 25% increase in global CO_2 concentrations, for example, may have implications for future forest growth responses. From tree ring studies, La Marche *et al.*[194] have reported an increase in growth of limber pine at western sites which they attribute to growth stimulation by increased CO_2 levels. Experiments by Norby *et al.*[199] suggest that tree growth will respond positively to increased CO_2 under nutrient-limiting soil conditions. Increased root growth and, in some experiments, increased uptake of aluminum and other trace metals were noted as CO_2 levels were increased to 700 ppm.

As interest in evaluating the consequences of atmospheric pollution on the stablility of forest systems increases, a better understanding of the plant- and ecosystem-level linkages between utilization processes involving carbon, water, and nutrient resources under anthropogenic stress will be needed. Such studies will necessitate the use of modeling approaches to examine multiprocess interactions. Whole-plant physiological models,[200] soil chemical models,[201] and forest growth and succession models[202,203] should be useful for integrating and projecting the effects of changes in system components to achieve a better understanding of whole-system response.

Because forest ecosystems are highly integrated and may be affected by pollutants through multiple pathways, it is unreasonable to assume that the role of regional-scale pollution in altering forest growth and stability will be easily identified or simply characterized. Forest responses to some stresses may take years to develop due either to the chronic nature of the stresses themselves or to the buildup of secondary pathogens on weakened hosts. While there is evidence of plant evolutionary adaptation to pollutant stress, the physiological, biogeochemical, and genetic adaptability of forest systems to current anthropogenic stresses has not been determined to date. The responses presently being observed in forests in industrialized countries may not be able to be quickly reversed even if air pollutants were conclusively shown to be at fault and immediate remedial action were taken.

Research during the past two to three years has added significantly to our knowledge of pollution effects on forests and provided important information on fundamental processes in forest systems as well. The questions of "How much more research?" and "How much more time?" are frequently asked and cannot be answered decisively at present. The next five years should see expanded programs of field and laboratory research substantially improve our present understanding of the extent, causes, and possibly the solutions for the changes in forest vigor observed in many countries. Decisions are now being made in some countries to reduce emissions based on information currently available on the nature and distribution of observed forest declines. Whether the costs and benefits of those decisions are in balance will only be determined by time, the resilience of forest systems, and additional focused research.

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